

Taxonomic revision of *Pisulina* (Gastropoda: Neritopsina) from submarine caves in the tropical Indo-Pacific

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Received 1 December 1999; Revised manuscript accepted 14 February 2000

Abstract. Species of the tropical Indo-Pacific gastropod *Pisulina* (superorder Neritopsina), previously known only from empty shells and regarded as a genus of Smaragdiinae (Neritidae), are revised on conchological criteria. *Pisulina* dwells in gloomy to totally dark, tropical and subtropical, shallow-water submarine caves, where their empty shells are ubiquitous. Study of the previously described modern and fossil species and examination of newly collected material from more than 50 submarine caves on Pacific islands show that there are six species in the genus: *P. adamsiana* Nevill and Nevill, 1869 (Holocene), *P. subpacificica* Ladd, 1966 (late Miocene), *P. biplicata* Thiele, 1925 (Recent), *P. maxima* new species (Recent), *P. tenuis* new species (Recent), and *Pisulina* sp. (Pleistocene). An analysis of previously unstudied shell characters (shell form, shell microstructure, protoconch morphology, and opercular features) of *Pisulina* and other modern, representative genera of Neritopsina places the genus close to the freshwater and brackish-water genus *Neritilia*, based on three unique characters (inclined protoconch, spiral ridges on the protoconch surface, and perpendicularly arranged prisms in the outer shell layer), and both genera are herein included in the family Neritiliidae. This study shows that the protoconch and shell microstructure analysis is important for re-evaluating fossil species previously placed in Neritidae.

Key words: Neritiliidae, *Pisulina*, protoconch, shell microstructure, submarine cave

Introduction

Pisulina Nevill and Nevill, 1869 has been a gastropod genus of systematically uncertain placement. Aside from the type species, *Pisulina adamsiana* Nevill and Nevill, 1869, the genus has included one modern species, *Pisulina biplicata* Thiele, 1925, and one fossil species, *Pisulina subpacificica* Ladd, 1966. The species previously have been known only from empty shells, so knowledge of their anatomy, operculum, radula and habitat have been entirely lacking. Empty shells occasionally have been found in beach drift from the tropical western Pacific (Habe, 1963; Hinoide and Habe, 1991; Fukuda, 1993; Loch, 1994; Sasaki, 1998) and have been dredged from 70 m off southern Africa (Herbert and Kilburn, 1991).

Nevill and Nevill (1869) thought the genus was close to

Teinostoma (currently classified in Vitrinellidae of Caenogastropoda; e.g., Ponder and de Keyzer, 1998) and *Calceolina* [junior synonym of *Teinostoma* (*Calceolata*); Thiele, 1929] based on overall similarity in shell morphologies. Thiele (1925) was the first author to place *Pisulina* in Neritidae, and this familial allocation was followed in his monograph (Thiele, 1929). Wenz (1938) included *Pisulina* in the subfamily Smaragdiinae Baker, 1923, of Neritidae, and was subsequently followed by Knight *et al.* (1960) and Komatsu (1986). However, Herbert and Kilburn (1991) found that *Pisulina* differs in protoconch morphology not only from *Teinostoma* but also from *Smaragdia*, the type genus of Smaragdiinae. They observed that the change of coiling axis occurs between the larval shell and teleoconch whorls in *P. adamsiana*, although they followed Robertson's (1971) view that this change occurs between the embryonic and

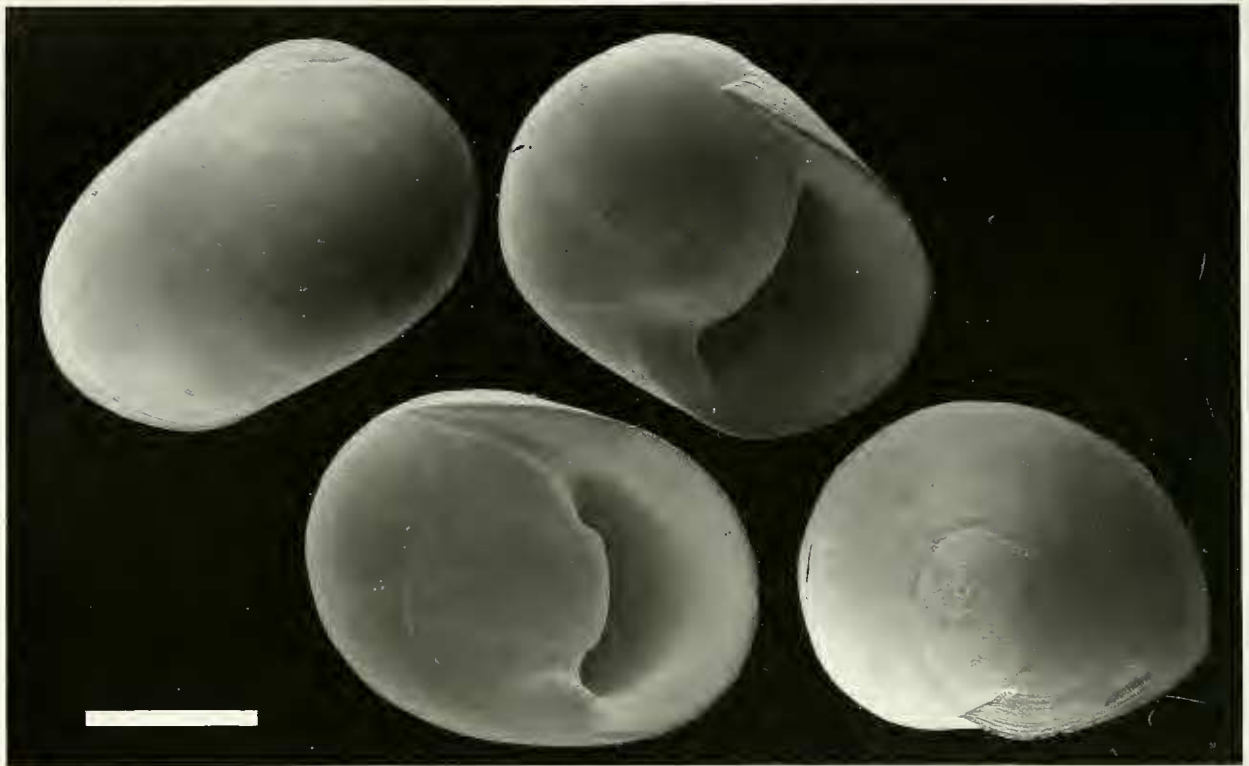


Figure 1. *Pisulina adamsiana* Nevill and Nevill, 1869 from Sipadan Island, Sabah, Malaysia (NSMT-Mo71619). Scale bar = 2 mm.

post-embryonic shells in *Smaragdia*. However, they did not elaborate on the systematic position of this enigmatic genus from their observations, and the systematic position of *Pisulina* has remained speculative.

Since 1989, the junior author and his co-workers have been conducting biological sampling in shallow-water submarine caves on tropical and subtropical Pacific islands with the help of skilled SCUBA divers. During the course of the sampling, they have found a molluscan community that is distinctive in species composition and reproductive biology (Kase and Hayami, 1992; Hayami and Kase, 1993, 1996). They also found that a huge number of empty shells of *Pisulina* species had accumulated in the bottom sediments in many caves, and that living animals were abundant on the walls and ceilings of several caves in Hawaii, Saipan, Palau, the Philippines and Malaysia.

The purpose of this paper is (1) to describe the conchological characteristics of *Pisulina* in detail, (2) to define the genus and discuss its systematic position based on conchological characteristics, (3) to review all previously known species of *Pisulina*, and (4) to describe new species.

Materials and methods

We examined more than 5000 empty shells of *Pisulina* species obtained from the bottom sediments of more than 50 submarine caves, tunnels, grottos or caverns (at depths

ranging from 1.3 to 55 m), on tropical and subtropical Pacific islands. We also examined shells in beach drift and dredged samples, and fossil shells from Henderson Island (the Pitcairn Group) and Niue Island (Cook Islands). In the descriptions given below, the "Material examined" headings refer to empty shells, unless otherwise stated. Living animals were obtained from walls inside caves and tunnels by hand, or by brushing the undersurface of coral rubble on the bottom sediments. Empty shells were obtained from the sediments (mainly calcareous mud) of the cave floors by hand sorting.

For comparison, we examined embryonic shells of *Neritilia rubida* (Pease, 1865) from Tahiti. In addition, live specimens of another *Neritilia* species [collected in a stream in Tabaru Valley, Yonaguni Island, Okinawa Prefecture, Japan; identified by Kubo and Koike (1992) as *N. rubida*] were kept in a freshwater aquarium, and embryonic shells were obtained after spontaneous oviposition and following development. In the aquarium, egg capsules which each retained only one embryo were laid in small pits on the undersurface of limestone cobbles taken from the original habitat. The veligers were hatched as embryonic shells after two weeks of oviposition.

We prepared specimens for SEM observation using standard techniques: shells were cleaned with an ultrasonic cleaner, dried, mounted on stages, coated with gold, and examined under a scanning electron microscope (JOEL T330A), or were examined in a low-vacuum mode without a

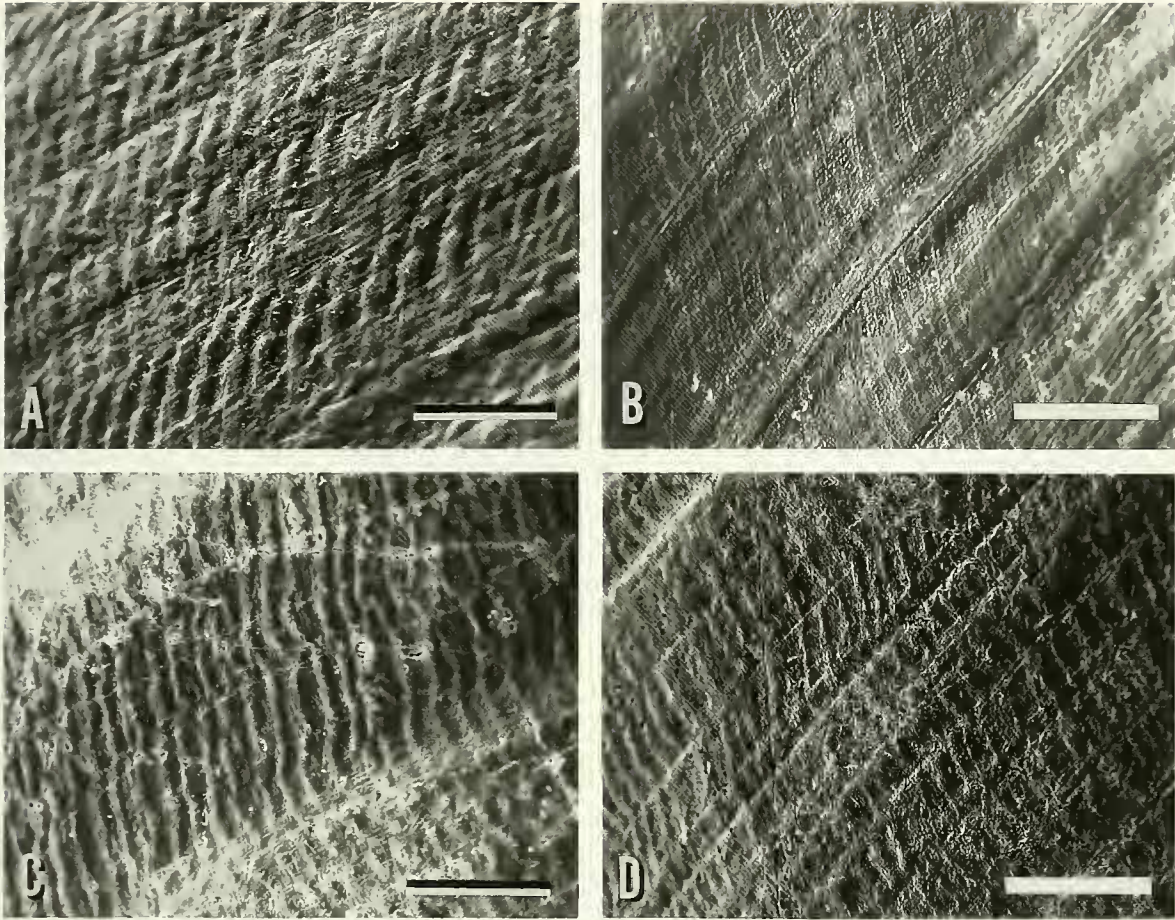


Figure 2. SEM micrographs of the subsutural surface of the last teleoconch whorls in four modern *Pisulina* species; all are oblique apical views. Scale bars = 50 μm . **A.** *Pisulina adamsiana* Nevill and Nevill from Sipadan Island, Malaysia. **B.** *Pisulina biphicata* Thiele from Shimoji Island, Okinawa, Japan. **C.** *Pisulina maxima* sp. nov. from Sipadan Island. **D.** *Pisulina tenuis* sp. nov. from Yonaguni Island, Okinawa.

metal coating in another SEM (JEOL 5200LV). Polished and etched sections were prepared for microstructural analysis of the shell wall in the following manner: blocks of shells were embedded in synthetic resin, polished, cleaned ultrasonically to remove polishing grit, etched in 0.3% acetic acid for 60 seconds, and cleaned again. The terminology and usage of shell ultrastructure follow Carter and Clark (1985).

Museum abbreviations. — AMS: Australian Museum, Sydney; MNHB: Museum für Naturkunde der Humboldt-Universität, Berlin; MNHN: Muséum National d'Histoire Naturelle, Paris; NSMT: National Science Museum, Tokyo; UMZC: University Museum of Zoology, Cambridge, England; USNM: National Museum of Natural History, Washington.

Systematic description

Superorder Neritopsina Cox and Knight, 1960
Family Neritillidae Schepman, 1908

Genus *Pisulina* Nevill and Nevill, 1869

Pisulina Nevill and Nevill, 1869, p. 160.

Type species. — *Pisulina adamsiana* Nevill and Nevill, 1869, by monotypy.

Distribution and age. — Tropical and subtropical Indo-Pacific. Late Miocene to Recent.

Diagnosis. — Shell small to medium in size, globose neritiform, white, smooth, solid. Inner lip of aperture smooth, convex, covered with a thick and widespread callus, with a robust projection or 3 to 7 teeth on margin. Outer lip with a weak inner ridge inside and a sharp margin. Protoconch either multispiral or paucispiral; multispiral

protoconch with a larval shell inclined approximately 30° to teleoconch axis, sculptured with several spiral ridges, and embryonic shell partially covered by larval shell whorls and also by first teleoconch whorl due to protoconch inclination. Outer layer of shell wall very thin, simple prismatic structure; each prism almost perpendicularly arranged to the outer shell surface. Operculum semicircular, paucispiral, thin, concave externally; external surface smooth, corneous, reddish straw in color; inner surface calcified except for marginal area, with an apophysis near base of inner margin.

General conchological features

Teleoconch.—The shell is small to medium in size, globose to subglobose or sometimes hemispherical, solid, white, and translucent when it is fresh (Figure 1). The teleoconch coils number less than four, increase rapidly in size, and have a less convex upper whorl surface. The suture is shallowly impressed. The last whorl is well inflated and has a round periphery. The exterior surface bears microscopic spiral ridges and very fine growth lines (Figure 2A–D). The aperture is small to large and crescent-shaped to semicircular in outline. The outer lip is prosocline, angled 30° to 50° from the shell axis, sharp along its margin, and is thickened interiorly into an indistinct inner ridge. The inner lip is covered with a smooth, thick and convex callus that spreads widely onto the base of the previous whorl. The adaxial margin of the inner lip bears a robust projection in *P. adamsiana* and *P. subpacific*, and three to seven teeth in all other species. The inner line of the callus surrounds the columellar area, then merges gradually with the basal lip. The inner walls of the whorls are resorbed, producing a hollow cavity inside (Figure 3), except for the last 1/3 whorl, where the cavity forms a relatively long, narrow, tube-like inner space and continues to the apertural opening. Inside the whorls is a funnel-like cavity which is separated from the main cavity by a steep wall and positioned just beneath the inner lip callus. This cavity, visible from the outside through the translucent inner lip callus, encases the distal end of an adapically projected digestive gland. Two muscle attachment scars are carved as shallow depressions; one corresponds to the left shell muscle of the animal, is spirally elongate and located beneath the convex part of the inner line of the aperture, while the other corresponds to the right shell muscle, is subcircular in shape and located close to the apex.

Protoconch.—The protoconch is deeply immersed in the first teleoconch whorl, separated from the teleoconch by a clear line of demarcation, and is either multispiral or paucispiral (Figures 4A–F; 5A–E). A multispiral protoconch,

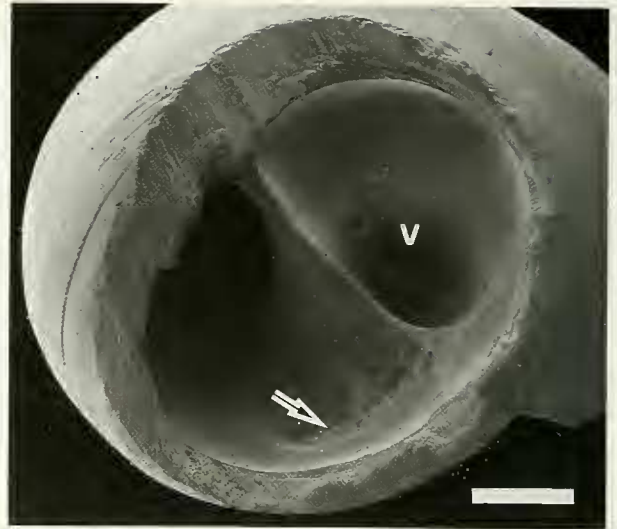
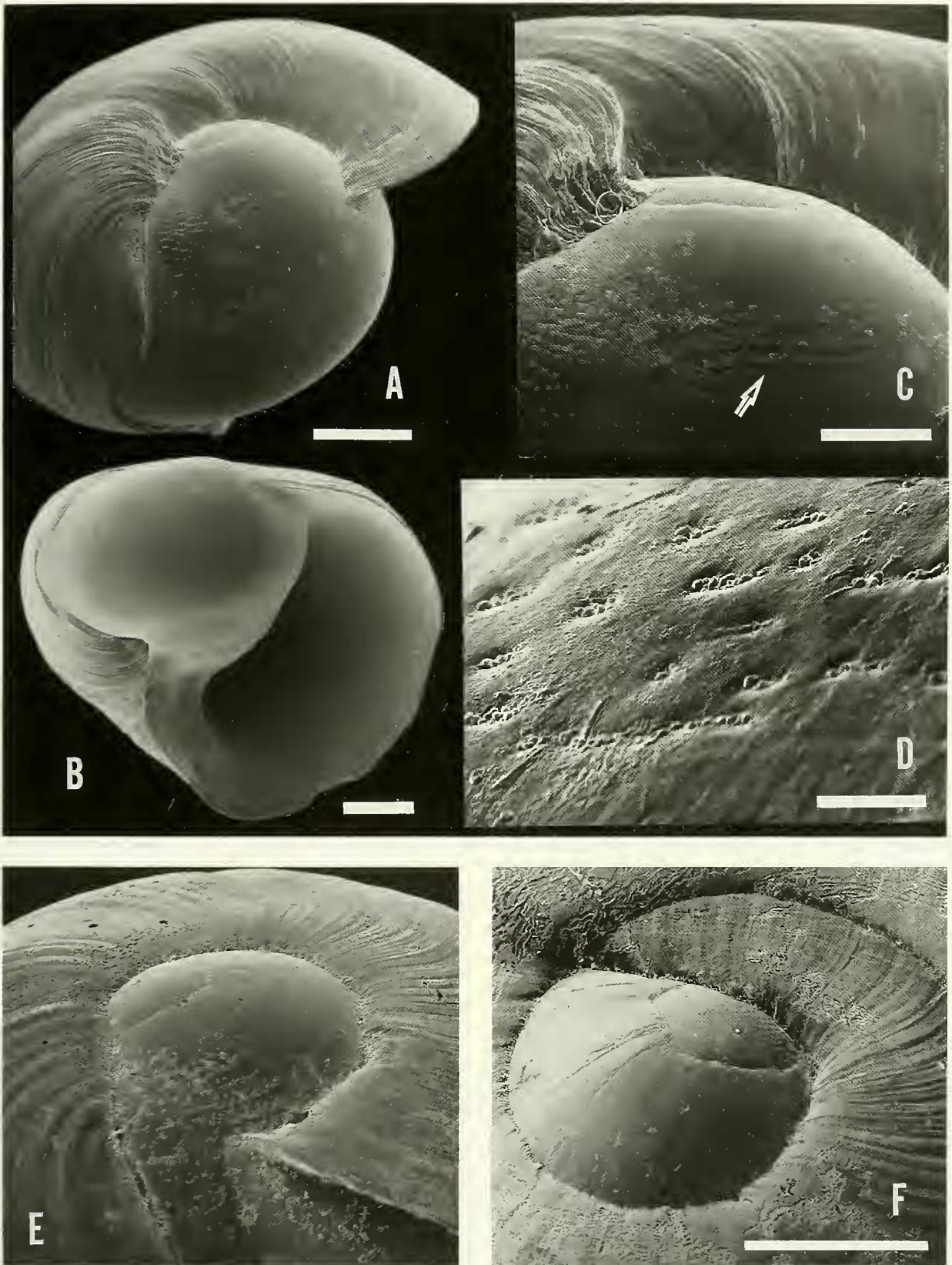


Figure 3. Shell (apical whorls removed) of *Pisulina adamsiana* Nevill and Nevill from South Kona, Hawai'i Island, showing the hollow internal space and the vertical cavity (v), the latter encasing the digestive gland of the animal; oblique apical view. Arrow indicates the elongate left muscle scar. Scale bar = 500 μ m.

seen in *P. adamsiana* and *P. subpacific*, consists of an embryonic shell (protoconch-I) and larval shell (protoconch-II). The embryonic shell is generally smooth and largely involved with the larval shell that bears four or five spiral ridges and many minute pits. The axis of the multispiral protoconch is sharply inclined (approximately 30°) compared to the teleoconch whorls, so the embryonic shell is partly covered by the initial teleoconch whorl (Figure 4A, E, F). The inner walls of the protoconch are resorbed into the teleoconch. A paucispiral protoconch, seen in some species, consists only of a large and smooth embryonic shell. In this case, the coiling axis of the protoconch appears to be the same as that of the teleoconch.

Shell microstructure.—The shell consists of three layers, excluding the myostracum, and Figure 7 shows their occurrence in the shell. The outermost layer (OL) is very thin (less than 20 μ m thick in *P. adamsiana*), and is composed of simple, irregular prisms (Figure 6A, B). Each prism is less than 2 μ m long, 0.3 μ m thick, and oriented with its long axis less than 10° to the outer shell surface. The middle layer (ML) is of very thick, simple crossed-lamellar structure (Figure 6A–D). The inner shell layer (IL) consists of alter-

Figure 4. SEM micrographs of the multispiral protoconch in *Pisulina adamsiana* Nevill and Nevill. All specimens came from off South Kona, Hawai'i Island. **A–D.** Juvenile specimen with 0.6 of a teleoconch whorl. **A.** Abapertural view showing the biconvex and opisthocline larval shell aperture. Scale bar = 100 μ m. **B.** Apertural view. Scale bar = 100 μ m. **C.** Detail of the apical area of the protoconch, oblique lateral view. Embryonic shell partly exposed. Arrow indicates spiral ridges on the shoulder of the larval shell. Scale bar = 50 μ m. **D.** Close-up of the larval shell surface near the aperture, showing the presence of granules within pits. Scale bar = 5 μ m. **E.** Oblique apical view of a juvenile specimen with 0.9 of a teleoconch whorl, showing faint spiral ridges on the larval shell surface. Scale bar = 100 μ m. **F.** Oblique apical view of an immature shell with 1.7 teleoconch whorls, showing wavy ridges on the embryonic shell surface that are visible due to a lesser degree of overlapping by the teleoconch whorl. Scale bar = 100 μ m.



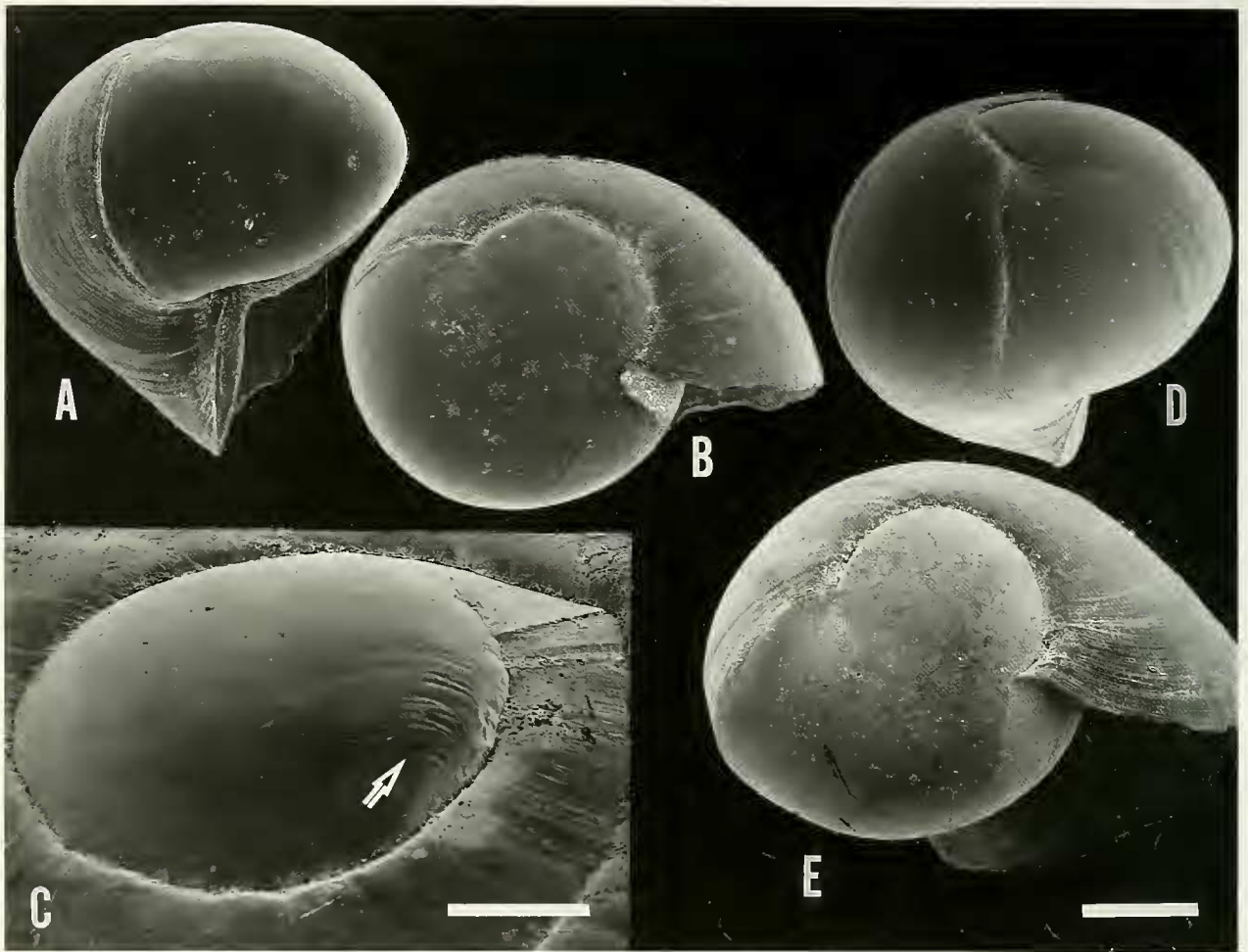
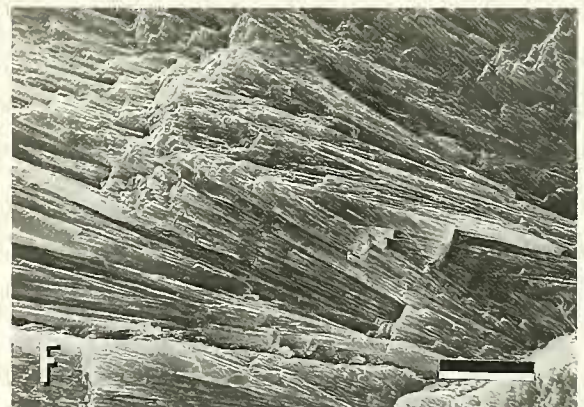
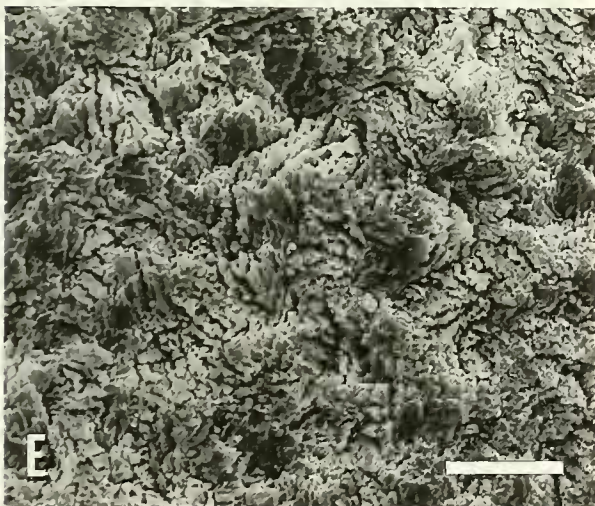
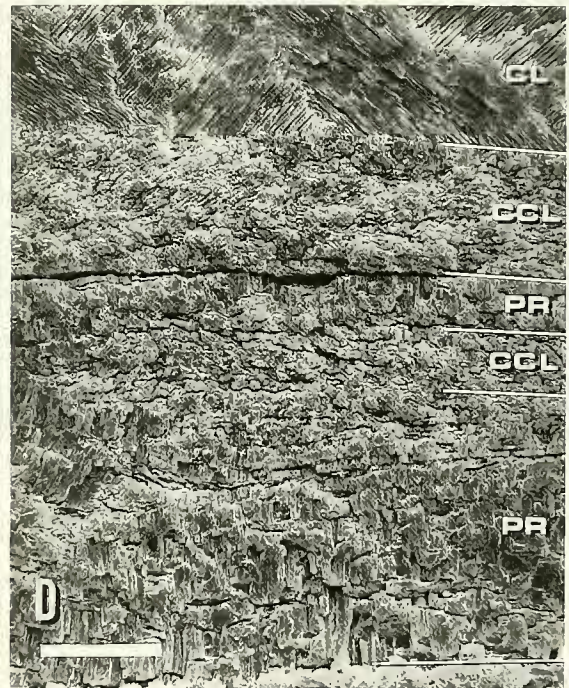
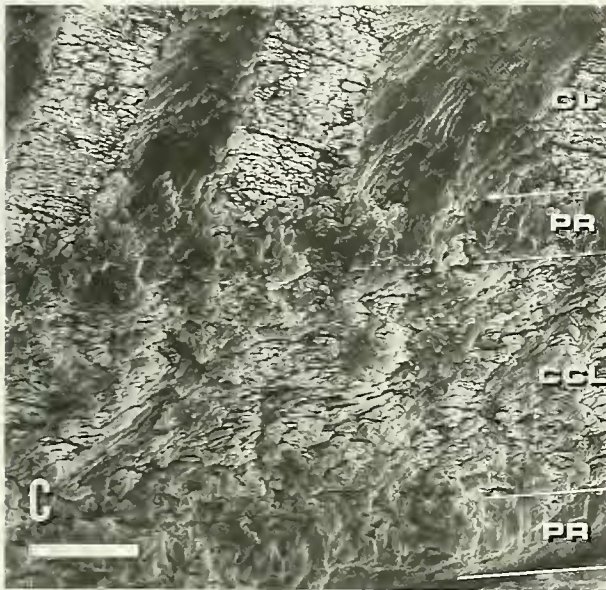
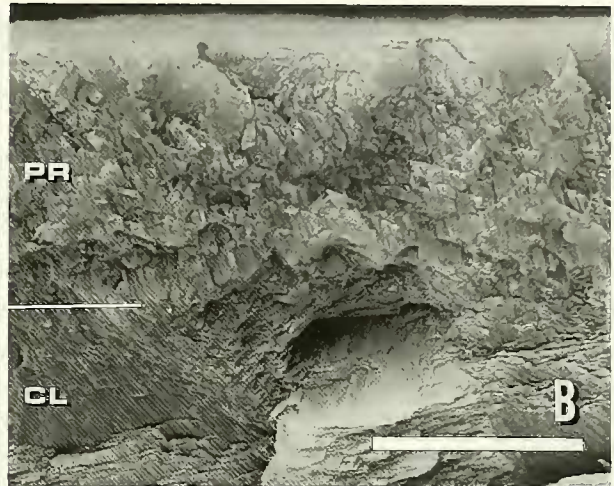


Figure 5. SEM micrographs of paucispiral protoconchs in *Pisulina* species. **A, B.** *Pisulina biplicata* Thiele, juvenile specimen with 0.5 of a whorl from off Kohama Island, Okinawa. Scale bar = 100 μm . **A.** Abapertural view. **B.** Slightly oblique apical view. **C.** *Pisulina maxima* sp. nov., oblique apical view of an immature specimen from off Aulong Island, Rock Islands, Palau. Arrow indicates longitudinal folds on the protoconch near the suture with the first teleoconch whorl. Scale bar = 50 μm . **D, E.** *Pisulina tenuis* sp. nov., juvenile specimens with 0.5 and 0.6 of a teleoconch whorl, respectively, from Yonaguni Island, Okinawa. Scale bar = 100 μm . **D.** Abapertural view showing transverse growth ridges near the protoconch aperture. **E.** Slightly oblique apical view.

Figure 6. SEM micrographs showing microstructures of the shell and operculum in *Pisulina adamsiana* Nevill and Nevill. **A.** Fractured shell surface of the outer lip of the aperture, cut perpendicular to the apertural margin, showing very thin outer prismatic layer and thick simple crossed-lamellar middle layer. The shell margin is to the right and the shell surface toward the top. Scale bar = 100 μm . **B.** Close-up of the fractured shell surface near the outer shell surface in A, showing details of the outer prismatic layer (PR) and the middle crossed-lamellar layer (CL). Scale bar = 10 μm . **C–E.** Etched surfaces of the section shown in Figure 7. **C.** The etched surface of an abapertural shell area, showing simple crossed-lamellar middle layer (CL) and inner layer. The inner shell surface faces toward the bottom. The inner layer consists of two irregular prismatic sublayers (PR) and an intervening complex crossed-lamellar layer (CCL). Scale bar = 10 μm . **D.** An etched shell surface near the back of the inner line of the inner lip shows the simple crossed-lamellar middle layer (CL) and the inner layer. The inner layer consists of alternating irregular prismatic sublayers (PR) and complex crossed-lamellar sublayers (CCL). Scale bar = 20 μm . **E.** Complex crossed-lamellar structure of the reconstructed inner shell wall. Scale bar = 10 μm . **F.** Fractured surface of an operculum, showing spherulitic prismatic structure. Scale bar = 10 μm .



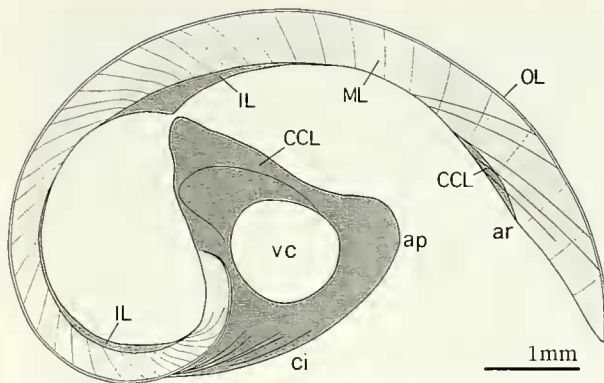


Figure 7. Arrangement of shell layers in *Pisulina adamsiana* Nevill and Nevill. The section is roughly perpendicular to the shell axis. Abbreviations: OL: very thin outer layer with prismatic structure; ML (light gray): thick middle layer with simple crossed-lamellar structure; IL (dark gray): inner layer made up of alternating sublayer(s) of complex crossed-lamellar and simple prismatic structures; CCL (dark gray): complex crossed-lamellar structure; ap: apertural projection; ar: apertural ridge; ci: callused inner lip of aperture; vc: vertical cavity.

nating sublayer(s) of complex crossed-lamellar and simple prismatic structure (Figure 6C, D). The prismatic sublayers consist of irregular prisms that are arranged vertically. The first-order lamellae of the complex crossed-lamellar structure are indistinct, variable in shape, and composed of a small number of thin, lath-like second-order lamellae (Figure 6E). The same shell structure is present in the robust inner lip area and in a small area just posterior to the inner ridge of the aperture, which are areas constructed secondarily after absorption of the original layers (CCL in Figure 7).

Operculum.—The operculum is semicircular in shape, with a minimum length/maximum length ratio of ca. 0.7, paucispiral, rather thin, and has a concave exterior surface (Figures 8A, B; 9A–C). The exterior surface fits well into the convex surface of the shell's inner lip when the animal fully extends its head-foot mass. The number of volutions may be up to 1.7, apart from the nucleus. The operculum consists of an outer corneous layer (up to 5 μm thick) and inner calcareous layers. The surface of the outer corneous layer is smooth (except for faint growth lines), reddish straw in color, and the color gradually becomes paler from the margin to nucleus. The nucleus appears only on the outer surface, is semicircular, located more or less abaxially and adapically from the center, paucispiral in *P. adamsiana* (Figure 8B) and concentric in the other modern species (Figure 9C). The inner surface of the operculum is calcified, except for the marginal area. The calcified area is covered with fine growth lines and bears a long apophysis near the base of the inner margin. The apophysis appears first as a weak ridge along the opercular suture, then becomes a curved calcified rod, and finally projects beyond the margin while remaining attached along its whole length to the basal margin of the operculum by a thin septum-like base. The muscle attachment scar can be divided into three areas: two are shallow, elongate depressions that are positioned at the



Figure 8. Operculum of *Pisulina adamsiana* Nevill and Nevill from Sipadan Island, Malaysia. **A.** Internal, lateral and external views (arranged from top to bottom). Scale bar = 500 μm . **B.** Oblique lateral view of the paucispiral nucleus on the external surface, showing 0.3 of a volution. Scale bar = 100 μm .

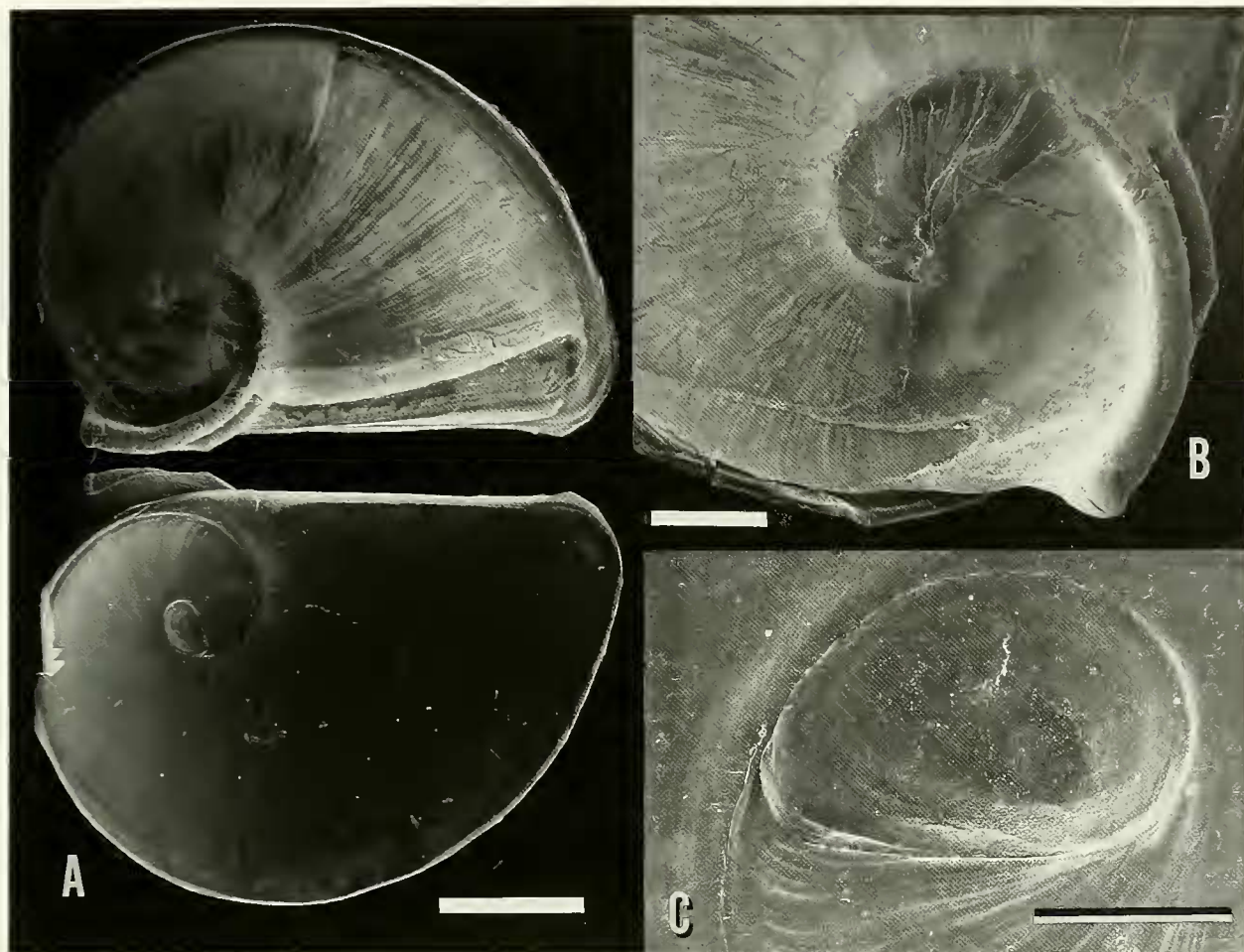


Figure 9. Operculum of *Pisulina maxima* sp. nov. from Sipadan Island, Malaysia. **A.** Internal (top) and external (bottom) views. Scale bar = 500 µm. **B.** Detail of apophysis and muscle attachments on the internal surface. Scale bar = 200 µm. **C.** Oblique view of the concentrically growing nucleus on the external surface of operculum. Scale bar = 100 µm.

inner and basal margins, and the other is between the apophysis and nucleus and is thicker than the other calcified areas due to having additional calcitic layers (Figure 9B). The calcareous part of the operculum is composed of spherulitic prisms (Figure 6F).

Systematic position of *Pisulina*

The protoconch morphology and shell microstructure of *Pisulina* are unique and almost identical to those of the freshwater genus of Neritopsina, *Neritilia* Martens, 1879; these are the only conchological characters useful for systematic placement.

Apart from species with non-planktotrophic development (see below), protoconchs of extant aquatic members of Neritopsina are quite uniform in shape and differ from those of all other gastropods (Bandel, 1982; Sasaki, 1998). The protoconchs of the following genera have been figured previ-

ously as SEM images: *Nerita* (Bandel, 1982; Sasaki, 1998), *Smaragdia* (Robertson, 1971; Bandel, 1982; Herbert and Kilburn, 1991), *Clithon*, *Neritina*, *Septaria* (Bandel and Riedel, 1998) [Neritidae]; *Phenacolepas* (Bandel, 1982; Sasaki, 1998), *Shinkailepas*, *Olgasolaris* (Beck, 1992) [Phenacolepadidae] and *Neritopsis* (Bandel and Frýda, 1999) [Neritopsidae]. These genera all share the same protoconch features: the embryonic shell is globular in shape, and the larval shell is oval to globular naticiform and has less than 3.5 volutions. As Bandel (1982) has noted, the larval shell is smooth except for fine growth lines, coils almost planispirally, and the suture line abuts the surface more adapical to the previous suture, so that the number of coils cannot be counted from the outside. Moreover, the inner walls of the larval shell are absorbed internally (*Neritopsis* is a possible exception; Bandel, 1992).

The protoconch of *Pisulina adamsiana* is fundamentally the same as in the Neritopsina mentioned above. However,

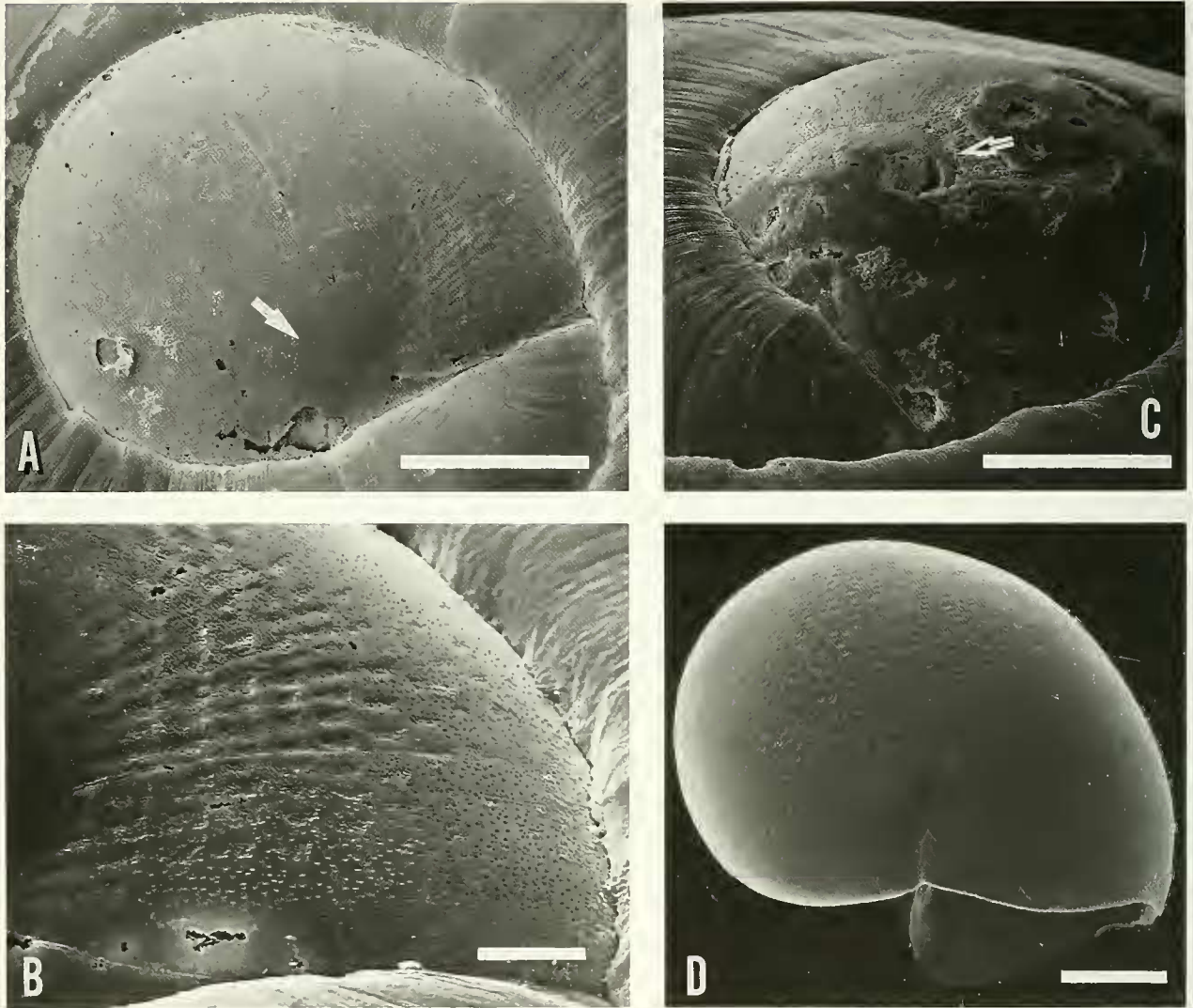


Figure 10. Multispiral protoconch and embryonic shell of *Neritilia*. **A–C.** Immature shells of *Neritilia rubida* (Pease) from Tahiti. **A.** Apical view of a juvenile shell with 1.2 teleoconch whorls. The surface is mostly intact. Arrow indicates the apex of the larval shell. Scale bar = 100 μm . **B.** Oblique close-up of the larval shell surface in A, showing the presence of spiral and axial ridges and minute pits entirely covering the protoconch surface. Scale bar = 20 μm . **C.** Oblique apertural view of juvenile shell with 1.2 teleoconch whorls. Outermost layer of the protoconch is partially eroded, so that the suture and growth lines of the larval shell are visible. Arrow indicates suture line. Scale bar = 100 μm . **D.** Apical view showing an embryonic shell of *Neritilia* sp. that was extracted from an egg capsule shortly before hatching. Part of the operculum protrudes from the aperture. Scale bar = 20 μm .

as already pointed out by Herbert and Kilburn (1991), the larval shell of *P. adamsiana* is distinctly tilted with respect to the teleoconch (Figure 4A–F). This tilting resulted from the change in direction of the growth lines from the larval shell (opisthocline) and the teleoconch whorls (prosocline). In addition, *P. adamsiana* has characteristic ridges (Figure 4A, C, E) and microscopic pits (Figure 4C, D) on the larval shell surface near the aperture (see description of *P. adamsiana*, below), which are sculptural features unknown in the other aquatic groups of Neritopsina.

We have found that members of the freshwater and brackish-water genus *Neritilia* have a protoconch almost identical to that of *P. adamsiana*, suggesting a close affinity between the two genera. Bandel and Riedel (1998) have already noted the unique protoconch morphology of *Neritilia* within the superfamily Neritoidea. The protoconch surface of the type species, *Neritilia rubida*, is smooth and has no suture line, so it appears to be a simple globular protoconch (Figure 10A, B). However, this is due to the subsequent laying down of a very thin calcareous layer over the surface of a



Figure 11. Oblique lateral view of a paucispiral nucleus with 0.3 of a volution on the operculum of *Neritilia* sp. from Yonaguni Island, Okinawa. Scale bar = 50 μ m.



Figure 12. Radula of *Pisulina maxima* sp. nov. from Sipadan Island, Malaysia. The radula is characterized by a large, strongly oblique outer lateral tooth and the absence of a central tooth, the features almost identical to that of *Neritilia* (see Baker, 1923). Scale bar = 50 μ m.

multispiral protoconch. In specimens whose protoconch surfaces are slightly eroded, the suture line and distinct growth lines are visible (Figure 10C), the once-hidden embryonic shell emerges close to the suture of the teleoconch, and a discontinuity in coiling is noticeable between the larval shell and teleoconch. The number of larval shell coils cannot be precisely counted, but appears to be about one, as seen in *P. adamsiana* (the paucispiral nucleus of the operculum, which is formed during the larval phase, is also similar to that of *P. adamsiana* in number of volutions; Figure 11). The calcareous layer over the protoconch appears to have been secreted after the last whorl of the larval shell was formed. In addition to the presence of this calcareous layer, *N. rubida* shows additional minor differences in its protoconch: the inclination of the coiling axis appears to be somewhat smaller, the larval shell has more numerous spiral ridges (five or six; Figure 10B) than *P. adamsiana*, and the microscopic pits are scattered all over the surface of both embryonic and larval shells without an evident pattern (Figure 10B, D). Bandel and Riedel (1998, fig. 6A, B) figured the protoconch of *Neritilia* sp. cf. *N. rubida*, from the Matutinao River, Cebu, the Philippines. The spirally arranged pits on the larval shell of this species differ from those described here for *N. rubida*. The spiral rows of pits in the Philippine *Neritilia* species evidently are a homologous character shared with *P. adamsiana*.

Shell microstructure is a second clue to the close relationship between *Pisulina* and *Neritilia*. Previous descriptions of shell microstructure of Neritopsina have been mostly restricted to Neritidae (e.g., Bøggild, 1930; Gainey and Wise, 1980; Bandel, 1990). The presence of a calcitic outer layer (with a homogeneous or prismatic structure) and aragonitic middle and inner layers (crossed-lamellar structure) are features shared among Neritopsina (e.g., Ponder and Lindberg, 1997:103). *Pisulina* has shell microstructure features that are basically the same as seen in Neritidae (Figures 6A–E;

7). However, *Pisulina* differs markedly from Neritidae in the inclination of prisms in the outer layer. The prisms are arranged almost perpendicularly in *Pisulina* (Figure 6B), while they are almost horizontal or very oblique relative to the exterior shell surface in neritids (Bøggild, 1930; Knight *et al.*, 1960:123; Bandel, 1990; personal observation). Although the outer prismatic layer is brown in color and much thicker than in *Pisulina*, *Neritilia rubida* shares characteristic features regarding the inclination and size of prisms with *Pisulina*.

The monogeneric family Neritiliidae was erected for the genus *Neritilia* by Schepman (1908) based upon its unique radular morphology. However, the genus has been assigned to the subfamily Neritiliinae of Neritidae (e.g., Baker, 1923; Thiele, 1929; Wenz, 1938; Knight *et al.*, 1960). Holthuis (1995) has recently shown the paraphyly of "Neritidae" and concluded that *Neritilia* is the sister group of Neritidae and Phenacolepadidae. Thus, *Neritilia* should be classified as an independent family of the superorder Neritopsina, namely Neritiliidae Schepman, 1908, rather than being placed in Neritidae.

Although the detailed systematic position of *Pisulina* must ultimately be determined by phylogenetic analysis based on conchological, anatomical, and molecular criteria, it is reasonable to conclude at present that *Pisulina* is not a member of Neritidae, but should be allocated along with *Neritilia* to Neritiliidae. The close relationship between the two genera is also confirmed by radular and anatomical characters (Figure 12; Kano and Kase, in preparation). We believe that the protoconch with the whorl inclination and spiral ridges, and the almost perpendicular prisms in the outer shell layer, are synapomorphies of *Pisulina* and *Neritilia*.

These synapomorphies are important criteria for re-



Figure 13. Paucispiral protoconch of *Neritopsis radula* (Linnaeus), juvenile specimen with 0.2 of a teleoconch whorl, from Yonaguni Island, Okinawa, in apical view. Bandel and Frýda (1999) illustrated a multispiral protoconch of *N. radula* from Mauritius. Further research is needed to resolve whether *N. radula* from the western Indian Ocean and Pacific are different species or an example of poecilogony (different early ontogenies within a single species; Bandel and Riedel, 1998), unknown among the Gastropoda. Scale bar = 100 μ m.

evaluating fossil species previously placed in Neritidae, which ranges in age from Triassic to Recent. Knight *et al.* (1960) recognized 19 fossil genera (4 are still living) in the family and diagnosed most genera solely on the basis of teleoconch characters. The apical whorls of fossil neritids tend to be lost by abrasion and/or dissolution, but in rare instances they are preserved intact in sediments deposited in low-energy, soft-bottom environments. By examining fossil species, we have found that two species, *Pisulinella miocenica* Kano and Kase, 2000, and "*Neritilia*" *tracyi* Ladd, 1965, both from the Miocene of the Marshall Islands, are undoubtedly members of Neritiliidae. As in *Neritilia* and *Pisulina*, these two species possess an inclined protoconch bearing spiral ridges, but differ from *Neritilia* and *Pisulina* in important ways (Kano and Kase, 2000; unpublished data).

Implications of paucispiral protoconch

Pisulina species have either a paucispiral or multispiral protoconch. Nevertheless, the species are undoubtedly closely related to one another, because of the many close similarities in other shell characters. We suggest that the paucispiral protoconch originated from the multispiral protoconch of an ancestral *Pisulina* species, as described below.

Most aquatic species of Neritopsina have a long planktotrophic duration after hatching from their egg capsule, and feeding veligers secrete a multispiral larval shell. However, species of some freshwater genera (e.g., *Theodoxus*) have a very large (ca. 0.9 mm) paucispiral protoconch and their development is quite different from that

of other members of Neritopsina. They undergo benthic development, and metamorphosis occurs within the egg capsule by means of nurse-egg feeding (Bandel, 1982). The juveniles crawl out from the capsule with their foot. According to Holthuis (1995), free-swimming veligers (ancestral for the group) were lost at least four times in the evolutionary history of Neritidae, and in *Nerita* and *Vitta* the loss occurred within the genus (or subgenus). The non-planktotrophic (benthic or lecithotrophic) development of *Pisulina* seems to have originated from a planktotrophic ancestor, after the origin of the genus, by exploiting an adaptive modification different from freshwater neritids. Benthic development is much more prevalent in freshwater invertebrates than in their marine relatives, because the downstream loss of freshwater larvae in moving water is the primary determinant for benthic development (Holthuis, 1995). Meanwhile, the non-planktotrophic development of *Pisulina* may be an adaptation to the unique cryptic environments in marine caves. Kase and Hayami (1992) and Hayami and Kase (1996) have shown that the predominance of non-planktotrophic development and the dominance of brooding species among submarine cave bivalves primarily resulted from an adaptation to food-limited conditions. Although no examples of this have been found in gastropods so far, it may be that *Pisulina* underwent non-planktotrophic development and acquired a paucispiral protoconch by adapting to a cryptic habitat. *Neritopsis radula* (Linnaeus, 1758), another cave-dwelling species of Neritopsina, developed a similar paucispiral protoconch (Figure 13).

It is worth noting that paucispiral and concentric opercular nuclei are connected with multispiral and paucispiral protoconchs. The paucispiral nucleus (the operculum of a veliger) grows during the planktotrophic period, while the concentric nucleus is formed in the egg capsule, providing an additional criterion for inferring the mode of development in gastropods.

Pisulina adamsiana Nevill and Nevill, 1869

Figures 1; 2A; 3-4; 6-8

Pisulina adamsiana Nevill and Nevill, 1869, p. 160, pl. 17, fig. 4; Thiele, 1925, p. 32, pl. 3, fig. 16; Thiele, 1929, p. 111, fig. 54; Wenz, 1938, p. 431, fig. 1060; Knight *et al.*, 1960, p. 285, fig. 185-3; Habe, 1963, p. 231, 232, fig. 1; Ladd, 1977, p. 14, 15, pl. 1, figs 1, 2; Herbert and Kilburn, 1991, p. 320-322, figs. 1-3; Hinoide and Habe, 1991, p. 49 (in part), fig. 1.

Material examined.—INDIA: "Calcutta"; 1 specimen, coll. Paetel, MNHB.—"Ganges River delta" (21°40'N, 88°00'E); pre 1913, 3 specimens, AMS C-034497.—MALDIVES: Ari Atoll; 25 m depth; January 1996; 1 specimen, coll. S. Gori.—JAPAN: "Shodokutsu (= small cave)", Ie Island, Okinawa (26°42.9'N, 127°50.1'E); 20 m depth, totally dark submarine cave; 1988; 12 specimens.—"Umagai" diving site, north of Hatenuhama, east of Kume Island (26°21.1'N, 126°53.1'E); 24-28 m depth, submarine caves, totally dark inside; July 1996, 2 specimens.—"Witch's House (= Majono-yakata)" diving site, northwest of Shimoji Island, Miyako Islands, Okinawa (24°49.3'N, 125°08.3'E); 35 m depth, submarine

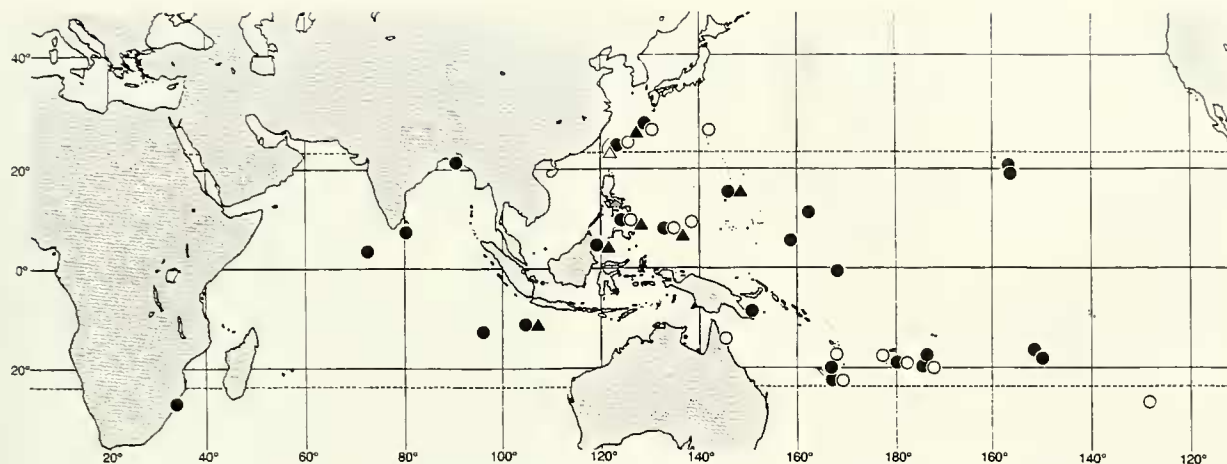


Figure 14. The geographic distribution of Recent *Pisulina* species. *Pisulina adamsiana* Nevill and Nevill (solid circles), *Pisulina biplicata* Thiele (open circles), *Pisulina maxima* sp. nov. (solid triangles) and *Pisulina tenuis* sp. nov. (open triangle). The type locality of *P. biplicata* is not plotted, because it was designated only as "Indian Ocean."

cave, totally dark inside; 54 specimens (10 specimens NSMT-Mo71618).—"Torিকে" diving site, northwest of Shimoji Island (24°49.1'N, 125°08.3'E); 12–40 m depth, several caves branching from a huge tunnel, gloomy to totally dark inside; 1992–1996, 2 specimens.—"Black Hole" diving site, northwest of Shimoji Island (24°49.1'N, 125°08.3'E); 35 m depth, submarine cave, totally dark inside; 1 specimen.—"Sabachi Cave", southeast of Yonaguni Island, Yaeyama Islands, Okinawa (24°26.1'N, 122°57.5'E); 25–30 m depth, submarine cave, totally dark inside; September 1994, 2 specimens.—MALAYSIA: "Turtle Cavern", Sipadan Island, west Celebes Sea, Sabah (5°04.8'N, 118°36.5'E); 9–17 m depth, totally dark inside; May 1997, 10 specimens (including 9 live individuals; 1 empty shell NSMT-Mo71619).—PHILIPPINES: "Marigondon Cave" diving site, Mactan Island, Cebu (10°15.8'N, 123°59.2'E); 27 m depth, large submarine cave, totally dark inside; May 1994, more than 1000 specimens; November 1998, 3 live specimens.—Balicasag Island, Panglao, Bohol (9°32.7'N, 123°40.7'E); 14–40 m depth; submarine caverns, gloomy inside; May 1994, 162 specimens (10 specimens NSMT-Mo71620).—"Mapatin Cave" diving site, southwest of Maricaban Island, Batangas, Luzon (13°40.0'N, 120°49.0'E); 46 m depth, lava tube, totally dark inside; November 1998, 1 live specimen.—PALAU: "Virgin Hole", west of Ngemelis Island, Rock Islands (7°07.3'N, 134°14.1'E); 17 m depth, submarine cave, totally dark inside; April 1995, 4 specimens.—"Siaes Tunnel" diving site, southwest of Siaes drop off, ca. 6 km west-northwest of Aulong Island, Rock Islands (7°18.7'N, 134°13.6'E); 24–53.5 m depth, huge submarine tunnel; April 1995, 141 specimens; December 1997, 19 specimens.—NORTHERN MARIANAS: near "Grotto" diving site, north of Saipan Island (15°15.3'N, 145°49.5'N); 12–30 m depth, huge cave, gloomy to totally dark inside; November 1997, 31 specimens (including 3 live individuals).—near "Tinian Grotto" diving site, west of Tinian Island; 50–51 m depth, huge cave, gloomy to totally dark; November 1997, 6 specimens.—POHNPEI: "Plang Point" diving site, west of Pohnpei Island (6°51.4'N, 158°

06.6'E); 55m depth, cavern, gloomy inside; November 1999, 2 specimens.—HAWAII: "Worm Cave", off Ahihi-Kinau, Makena, Maui Island (20°35.3'N, 156°25.8'W); 26–31 m depth, submarine cave, gloomy to totally dark inside; October 1997, 54 specimens (including 5 live individuals).—"Lost Crater Caves" diving site, off Ahihi-Kinau (20°35.3'N, 156°25.7'W); 25 m depth, submarine lava cave, gloomy inside; October 1997, 1 live individual.—"Long Lava Tube", off Pali Kaholo, South Kona, Hawai'i Island (19°21.8'N, 155°56.8'W); 11 m depth, long lava tunnel, gloomy; November 1997, 16 specimens.—"Gustav Cave", off Ka'u Loa Point, South Kona (19°19.1'N, 155°53.2'W); 6–8 m depth, submarine cave, gloomy to totally dark inside; November 1997, 19 live individuals.—PAPUA NEW GUINEA: between Magulata and Kabuluna Points, Kiriwina Island, Trobriand Group (8°27'S, 150°59'E); 73 m depth, coral sand bottom, outside outer reef; June 1970, 1 specimen, coll. W. F. Ponder and P. H. Colman, AMS C-345150.—NAURU: Aiwo (0°32.6'S, 166°54.5'E); 15–25.5 m depth, cavern, open to gloomy inside; November 1999, 43 specimens.—AUSTRALIA: "Hangover Cave" diving site, west of Direction Island, Cocos (Keeling) Islands (12°06.3'S, 96°52.5'E); 51–52.3 m depth, cavern, gloomy inside; December 1999, 4 specimens.—"Boat Cave" diving site, Christmas Island; 2.4 m depth; totally dark inside; November 1999, 1 specimen.—"Thunder Dome" diving site, Christmas Island; 7.7–10.2 m depth, long cave, totally dark inside; December 1999, 12 specimens.—NEW CALEDONIA: east of Nuu Poa islet, Iles des Pins, New Caledonia (22°31.6'S, 169°25.8'E); 17–19.5 m depth, meandering submarine cave, gloomy inside; October 1996, 3 specimens, MNHN.—FIJI: north of Ono Island, Great Astrolabe reef (18°51.8'S, 178°27.0'W); 7–16 m depth; submarine tunnel, gloomy inside; December 1996, 2 specimens.—northwest of Dravuni Island, Great Astrolabe reef (18°45.3'S, 178°28.0'W); 23–24 m depth; December 1996, 18 specimens.—TONGA: north of Haano Island, Ha'apai Group (19°38.2'S, 174°18.0'W); 44 m depth, cavern; December 1996, 6 specimens.—west of Mo'ung'one Island, Ha'apai

Table 1. Comparison of shell characters in five species of *Pisulina*. Some of the character states in *Pisulina subpacificica* Ladd (those shown in parentheses) may not represent general features of the species, owing to the immature condition of the holotype.

Species	Shell diameter of largest specimen	Shell thickness	Width of ridges on teleoconch surface	Apertural width	Number of inner lip teeth
<i>Pisulina adamsiana</i>	6.7 mm	thick	ca. 7µm	small	1
<i>Pisulina subpacificica</i>	(1.2 mm)	thick	?	small	1
<i>Pisulina buplicata</i>	4.8 mm	thick	ca. 1µm	small	3-5
<i>Pisulina maxima</i> sp. nov.	13.7 mm	very thick	ca. 4µm	very large	3-7
<i>Pisulina tenuis</i> sp. nov.	4.0 mm	thin	ca. 4µm	large	4-5

Species	Situation of inner line near base	Tubercle on basal lip	Protoconch coiling	Max. dimension of protoconch exposed above teleconch
<i>Pisulina adamsiana</i>	absent	present	multispiral	155-215µm
<i>Pisulina subpacificica</i>	absent	(absent)	multispiral	275µm
<i>Pisulina buplicata</i>	present	absent	paucispiral	155-220µm
<i>Pisulina maxima</i> sp. nov.	present	absent	paucispiral	180-275µm
<i>Pisulina tenuis</i> sp. nov.	present	absent	paucispiral	210-300µm

Group (19°23.2'S, 174°28.6'W); 20.5–37.5 m depth, submarine cave, totally dark inside; December 1996, 1 specimen.—"Sea Fans Cave" diving site, east of Taungiskika Island, Vava'u Group (18°39.7'S, 174°04.2'W); 7 m depth, submarine cave, gloomy inside; December 1996, 9 specimens.—SOCIETY ISLANDS: Tetuatiare Passage, north of Raiatea (16°49.5'S, 151°29.6'W); 10 m depth; submarine caves, gloomy inside; December 1996, 1 specimen, MNHN.—"Cave Arue" diving site, west of Tahiti Island (17°30.9'S, 149°32.1'W); 22–30 m depth; submarine caves, gloomy inside; December 1996, 12 specimens, MNHN.—"Banc des Daulphins" diving site, west of Tahiti Island (17°29.9'S, 149°38.3'W); 20 m depth; submarine cavern, gloomy inside; December 1996, 103 specimens (50 specimens registered; MNHN).

Distribution and age.—Tropical and subtropical Indo-Pacific (Figure 14). Holocene.

Diagnosis.—Medium-sized *Pisulina* characterized by a thick, globose to obliquely ovate shell, a robust projection on inner lip, and ca. 7 µm-wide wavy spiral ridges over teleoconch surface; protoconch multispiral, with exposed portion drop-shaped and 155 to 215 µm in maximum dimension; larval shell with 3 or 4 spiral ridges and many microscopic pits; inner line of inner lip callus continuous with basal lip without a sinus; basal lip with a weak tubercle.

Description.—Shell small, up to 6.7 mm wide and 7.0 mm high, thick, globose to obliquely ovate, with a low spire and a blunt apex (Figure 1). Protoconch multispiral. Embryonic shell covered by larval shell whorls and by first teleoconch whorl to varying degrees based on protoconch inclination, smooth, sometimes with faint wavy ridges near teleoconch suture (Figure 4F); exposed portion of embryonic shell 70 to 90 µm in maximum dimension. Larval shell coils about 1 volution, surrounded largely by first teleoconch whorl, obliquely ovate, about 360 µm wide and 250 µm high,

inclined about 30° to teleoconch (Figure 4A, B, E, F); exposed drop-shaped area 155–215 µm in maximum dimension, almost smooth except for unevenly spaced growth lines; surface near apertural lip sculptured with 3 or 4 indistinct, ca. 3 µm-wide, 80 to 140 µm-long spiral ridges (Figure 4C), and also with many pits more or less irregularly arranged in a spiral direction and sometimes giving rise to short grooves (bearing granules up to 0.5 µm in diameter) by being connected with one another (Figure 4D). Apertural lip of larval shell biconvex, opisthocline and very discordant with first teleoconch whorl (Figure 4A). Teleoconch coils less than 3.3 in number, smooth to somewhat polished, first whorl coils almost planispirally; teleoconch surface with dense, ca. 7 µm-wide spiral ridges, subdivided by growth lines (Figure 2A). Aperture narrow and semilunar; outer lip prosocline, angled 35° to 40° to shell axis, beveled and not reflected; inner lip thickened by callus, with a broad, strong, quadrangular projection at its middle and a weak tubercle on the base; inner line of inner lip callus is an inverse-S shape, without situation at base. Operculum (Figure 8A) with a paucispiral nucleus 215 to 230 µm in maximum dimension (Figure 8B); apophysis moderately long and weakly curved spirally.

Remarks.—According to Herbert and Kilburn (1991), the holotype from Southern Province of Sri Lanka (Ceylon) is thought to be in the Indian Museum, Calcutta. We have not examined the type specimen, but there is little possibility of mistaking the shells at hand with any but this remarkable species.

Pisulina adamsiana is a quite distinctive species because it has a single robust quadrangular projection on the inner lip, whereas other modern species have multiple teeth. Moreover, this is the only modern species with a multispiral protoconch (Figure 4) and a paucispiral opercular nucleus (Figure 8B), which strongly suggest a relatively long



Figure 15. *Pisulina subpacificica* Ladd, 1966. Holotype (USNM 648341). Scale bar = 1 mm.

planktotrophic period for this species (see below). Furthermore, *P. adamsiana* differs from other *Pisulina* species by the inner line of its inner lip callus being inversely S-shaped, by the lack of a situation between the basal lip and the inner line of the inner lip callus, and by the presence of a weak tubercle on its basal lip (see Table 1).

Intraspecific variation of shell characters is small in this species, perhaps because of genetic homogeneity related to its well-developed dispersion ability. Scheltema (1971) estimated the duration of pelagic stage less than 55 days for *Smaragdia viridis* (Linnaeus, 1758). Taking the smaller size and fewer number of the larval shell whorls into consideration, the planktotrophic period of *P. adamsiana* is assumed to be shorter than that of *S. viridis*.

Koike (1985) described the spermatozoon ultrastructure of "*P. adamsiana* (?)" and stated that the spermatozoon is similar to that in *Clithon retropictus* (Martens, 1879), *Neritina plumbea* Sowerby, 1855, *Neritina variegata* Lesson, 1830, and *Septaria porcellana* (Linnaeus, 1758). However, the sperm of *P. adamsiana* from Sipadan Island is similar to the sperm of *Waldemaria* in Helicinidae rather than to the sperm of neritids (J. Healy, personal communication). It is likely that Koike's (1985) identification of *P. adamsiana* is incorrect.

Pisulina subpacificica Ladd, 1966

Figure 15

Pisulina subpacificica Ladd, 1966, p. 59, pl. 11, fig. 10.

Material examined.—Holotype from Bikini Island, Bikini Atoll, Marshall Islands; horizon in drill hole, at a depth of 789–799 feet (240–244m), late Miocene, USNM 648341.

Distribution.—Marshall Islands, known only from the type locality. Late Miocene.

Diagnosis.—Small *Pisulina* characterized by a globose and thick shell, a semilunar aperture and a strong quadrangular projection on inner lip; exposed portion of protoconch drop-shaped, ca. 275 μ m in maximum dimension.

Description.—Shell minute, 1.2 mm wide, 1.4 mm high, globose, thick, eroded, creamy in color, opaque, with a very low spire (Figure 15). Protoconch surrounded by first teleoconch whorl, drop-shaped in apical view, and visible portion is ca. 275 μ m in maximum dimension. Teleoconch of 1.5 whorls, with first whorl coiled almost planispirally; exterior surface lacking visible sculpture. Aperture small and semilunar in shape; outer lip prosocline, angled 35° to shell axis; inner lip thick and blunt at margin due to erosion, bearing a large, robust, adaxially convex quadrangular projection ca. 310 μ m wide and ca. 120 μ m high at its midpoint; inner line of inner lip callus inversely S-shaped, strongly concave in parietal area, and continues to basal lip without situation.

Remarks.—This Miocene species is known only from the holotype. *Pisulina subpacificica* is very similar to *P. adamsiana* in having a large, broad and quadrangular projection on its inner lip. Moreover, the present species seems to possess a multispiral protoconch as seen in *P. adamsiana*, judging from the drop-shaped protoconch that is exposed above the first teleoconch. Ladd (1966) separated this species from *P. adamsiana* based on its smaller shell size and lower spire, but the holotype of *Pisulina subpacificica* is unequivocally an immature specimen so these differences cannot be used to separate the two species. Fortunately, there are two characteristics that convincingly separate these two species. In *P. subpacificica*, the maximum dimension of the exposed portion of the protoconch is much larger (Table 1), and the inner lip projection is much stronger and twice as large as in *P. adamsiana*.

Pisulina biphlicata Thiele, 1925

Figures 2B; 5A, B; 16; 17A

Pisulina biphlicata Thiele, 1925, p. 32, pl. 3, fig. 15.

Pisulina adamsiana Nevill and Nevill. Komatsu, 1986, p. 42, 43, pl. 8, fig. 9; Hinoide and Habe, 1991, p. 49 (in part), fig. 2; Fukuda, 1993, p. 31, fig. 120; Sasaki, 1998, p. 117, figs. 78g, h.

Material examined.—Holotype from Indian Ocean ("East India?"), coll. von Finsch, MNHB.—JAPAN: Tsuchihama, Amami-Ohshima Island, Kagoshima (28°24.4'N, 129°21.1'E); beach drift; July 1991, 14 specimens.—March 1993, 18 specimens.—Sankakubama, Naze-shi, Amami-Ohshima Island (28°23.1'N, 129°30.3'E); beach drift; July 1991, 36 specimens.—Ankyaba, Kakeroma Island, Amami Islands

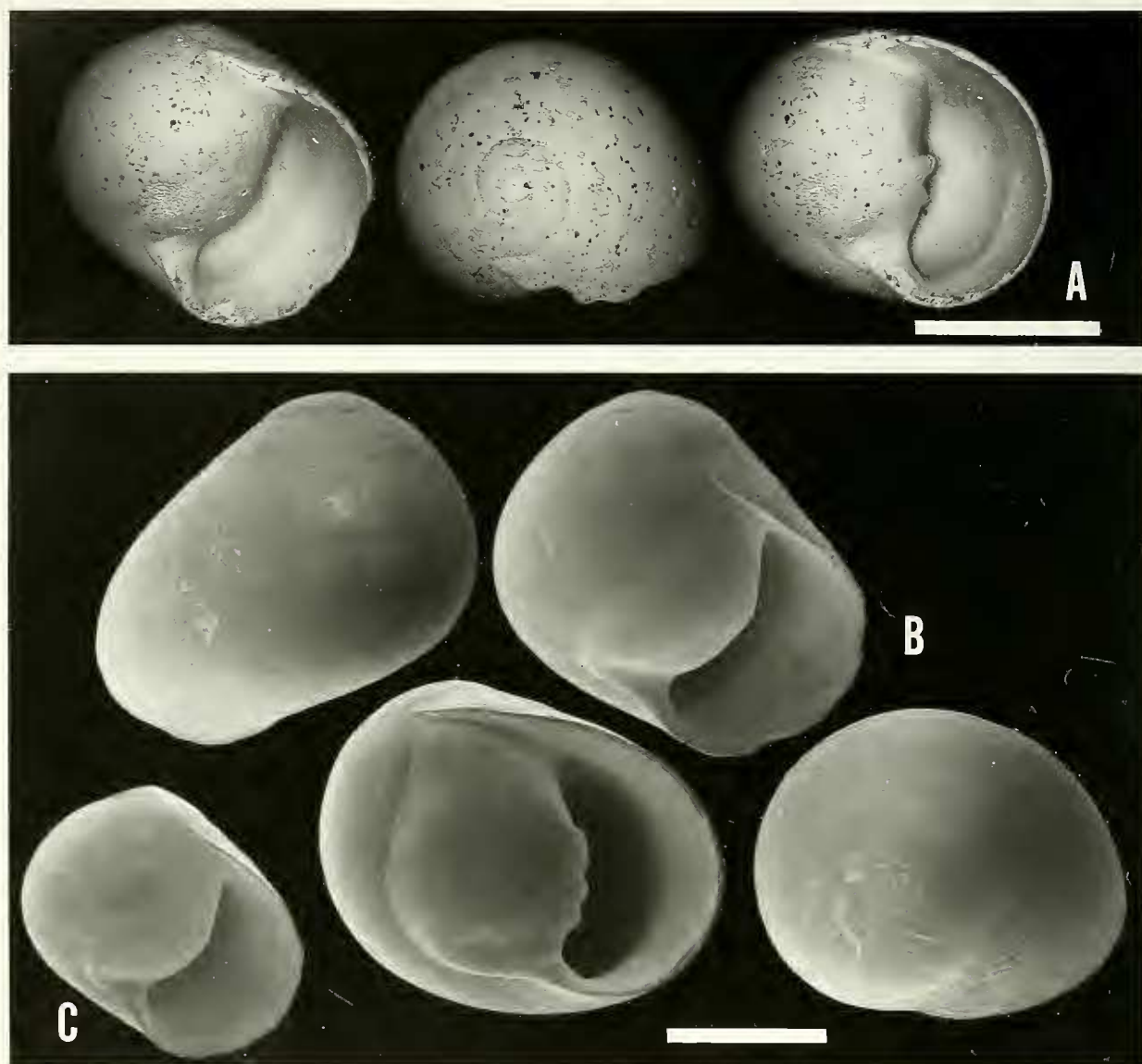


Figure 16. *Pisulina biplicata* Thiele, 1925. **A.** Holotype (MNHB), juvenile shell. Scale bar = 1 mm. **B.** Mature shell (four views) from Shimoji Island, Okinawa (NSMT-Mo71621). **C.** Mature shell (lower left specimen only) from Yap Island (NSMT-Mo71623). Scale bar = 2 mm for B and C.

(28°06.2'N, 129°21.1'E); beach drift; August 1993, 18 specimens.—Kunigami, Okinoerabu Island, Amami Islands (27°25.9'N, 128°42.8'E); beach drift; August 1992, 3 specimens.—"Devil's Palace (= Mao-no-kyuden)" diving site, Shimoji Island, Miyako Islands, Okinawa (24°49.7'N, 125°08.2'E); 25 m depth, submarine tunnels, gloomy inside; 1992, 93 specimens (10 specimens NSMT-Mo71621).—"Cross Hole" diving site, northwest of Irabu Island, Miyako Islands (24°51.6'N, 125°09.5'E); 15 m depth, submarine cave gloomy inside; 4 specimens, coll. M. Taniguchi.—north of Kohama Island, Yaeyama Islands (24°21.5'N, 123°58.9'E); 15–20 m depth, crevices; March 1996, more than 1000

specimens (20 specimens NSMT-Mo71622).—off Nishinohama, Kuroshima Island, Yaeyama Islands (24°14.6'N, 123°59.0'E); 10 m depth, sandy bottom; March 1996, 1 specimen.—PHILIPPINES: Balicasag Island, Panglao, Bohol (9°32.7'N, 123°40.7'E); 14–40 m depth; submarine caverns, gloomy inside; May 1994, 56 specimens.—PALAU: "Siaes Tunnel" diving site, southwest of Siaes dropoff, ca. 6 km west-northwest of Aulong Island, Rock Islands (7°18.7'N, 134°13.6'E); 24–53.5 m depth, huge submarine tunnel; April 1995, 3 specimens.—YAP: "Spanish Wall" diving site, west of Gilman, Yap Island (9°27.2'N, 138°02.5'E); 20–24 m depth, caverns and a small tunnel; November 1997, 18

specimens (6 specimens NSMT-Mo71623).—"Big Bend" diving site, west of Kanifay, Yap Island (9°28.1'N, 138°02.8'E); 8 m depth, a small cave, gloomy inside; November 1997, 4 specimens.—AUSTRALIA: Michaelmas Cay, Great Barrier Reef, Queensland (16°36'S, 145°59'E); May to June 1926, 1 specimen, coll. T. Iredale and G. P. Whitley (G. B. R. Boring Expedition), AMS C-345143.—Green Island, Great Barrier Reef (16°46'S, 145°58'E); May 1926, 1 specimen, coll. T. Iredale (G. B. R. Expedition), AMS C-345144.—East Face, Lizard Island, Great Barrier Reef (14°40'S, 145°29'E); 20 m depth; December 1974, 1 specimen, coll. W. F. Ponder, P. H. Colman and I. Loch, AMS C-345145.—NEW CALEDONIA: east of Nuu Powa islet, Iles des Pins, New Caledonia (22°31.6'S, 169°25.8'E); 17–19.5 m depth, meandering submarine cave, totally gloomy inside; October 1996, 2 specimens, MNHN.—Noumea (22°16'S, 166°27'E); pre-1950, 1 specimen, coll. T. Iredale, AMS C-345147.—VANUATU: White Sands, ca. 40 km from Port Vila, southeast of Efate Island (17°47'S, 168°33'E); March 1975, 2 specimens, coll. P. H. Colman, AMS C-345148.—west of Efate Island (17°39.1'S, 168°11.3'E); cavern; October 1996, 1 specimen.—"Taj Mahal" diving site, west of Efate Island (17°38.4'S, 168°08.7'E); 18 m depth, submarine cave, gloomy to totally dark inside; October 1996, 7 specimens.—FIJI: Nadi Bay (Tomba Ko Nandi), Viti Levu Island (17°44'S, 177°25'E); 9–35 m depth; 1962, 2 specimens, coll. J. Laseron, AMS C-345149.—northwest of Dravuni Island, Great Astrolabe reef (18°42.5'S, 178°29.8'W); 8 m depth, submarine cave, totally dark inside; December 1996, 1 specimen.—northwest of Dravuni Island, Great Astrolabe reef (18°45.3'S, 178°28.0'W); 23–24 m depth, cavern, gloomy to totally dark inside; December 1996, 5 specimens.—north of Ono Island, Great Astrolabe reef (18°51.8'S, 178°27.0'W); depth 7–16 m, submarine tunnel, gloomy inside; December 1996, 13 specimens.—TONGA: east of Fao Island, Ha'apai Group (19°46.5'S, 174°22.6'W); 6–7.5 m depth, submarine tunnel, gloomy inside; December 1996, 2 specimens.—southwest of Mo'ung'one Island, Ha'apai Group (19°38.3'S, 174°29.6'W); 11–28 m depth, cavern; December 1996, 3 specimens.—PITCAIRN GROUP: North Beach, Henderson Island; middle or late Pleistocene sediments in an uplifted cave; 1 specimen, coll. R. C. Preece (Pitcairn Islands Scientific Expedition 1991–2), UMZC.

Distribution and age.—Tropical and subtropical areas of the Indo-Pacific (Figure 14). Middle or late Pleistocene to Recent.

Diagnosis.—Medium-size *Pisulina* characterized by a glossy, thick, globose to pear-shaped shell, a high conical spire, a paucispiral protoconch, a semilunar aperture, and 3 to 5 blunt, somewhat squarish teeth along inner lip; teleoconch surface with microscopic spiral rows of granules.

Description.—Shell small, up to 4.8 mm wide and 5.5 mm high (1.7 mm wide and 1.6 mm high in holotype; Figure 16A), thick, globose to pear-shaped, with a moderately low to rather high conical spire (Figure 16B, C). Protoconch paucispiral, coiling almost planispirally with a slightly angulate periphery, ca. 310 μ m wide and ca. 250 μ m high, not inclined with respect to teleoconch (Figure 5A, B); outer lip of protoconch with faint and fine growth lines, remainder of protoconch smooth except for 15 to 25 indistinct longitudi-

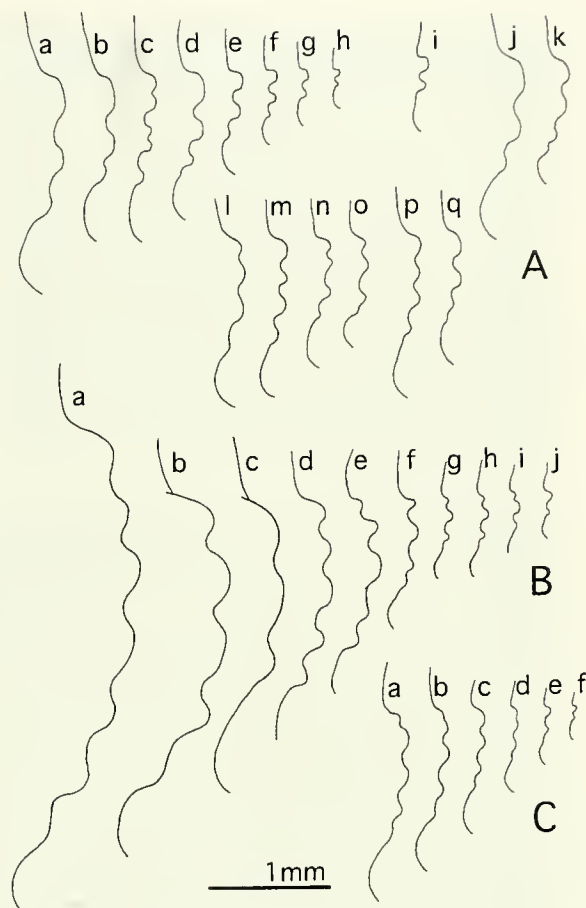


Figure 17. Ontogenetic changes in the apertural teeth of individuals of three *Pisulina* species from different geographic regions, seen in oblique apertural view. **A.** *Pisulina biplicata* Thiele, **a–h:** from Okinawa, **i:** Indian Ocean (Holotype), **j:** the Philippines, **k:** Palau, **l–o:** Yap, **p–q:** Fiji. **B.** *Pisulina maxima* sp. nov., **a:** Saipan Island (Holotype), **b:** the Philippines, **c–j:** Palau. **C.** *Pisulina tenuis* sp. nov., **a–f:** Okinawa.

nal folds; protoconch aperture longitudinally straight and clearly demarcated from teleoconch; visible portion of protoconch 155 to 220 μ m in maximum dimension (ca. 170 μ m in holotype). Teleoconch of up to 3.3 whorls (2.2 in holotype); last whorl inflated and with a small, somewhat concave area below suture; exterior surface smooth and glossy, but weakly sculptured with faint growth lines and microscopic spiral ridges (ca. 1 μ m wide; Figure 2B), consisting of rows of minute granules. Aperture semilunar, small; outer lip prosocline, angled 40° to 50° to shell axis and beveled; inner lip heavily callused with 3 to 5 rather blunt and somewhat squarish teeth at margin (Figure 17A); inner line of inner lip callus convex on columellar area, and continues toward the basal lip with a shallow sinus.

Remarks.—The shell of *P. biplicata* is frequently found as beach drift in southern Japan, but live specimens have not been found. Several opercula most probably from *P. biplicata* have been found together with more than 1000

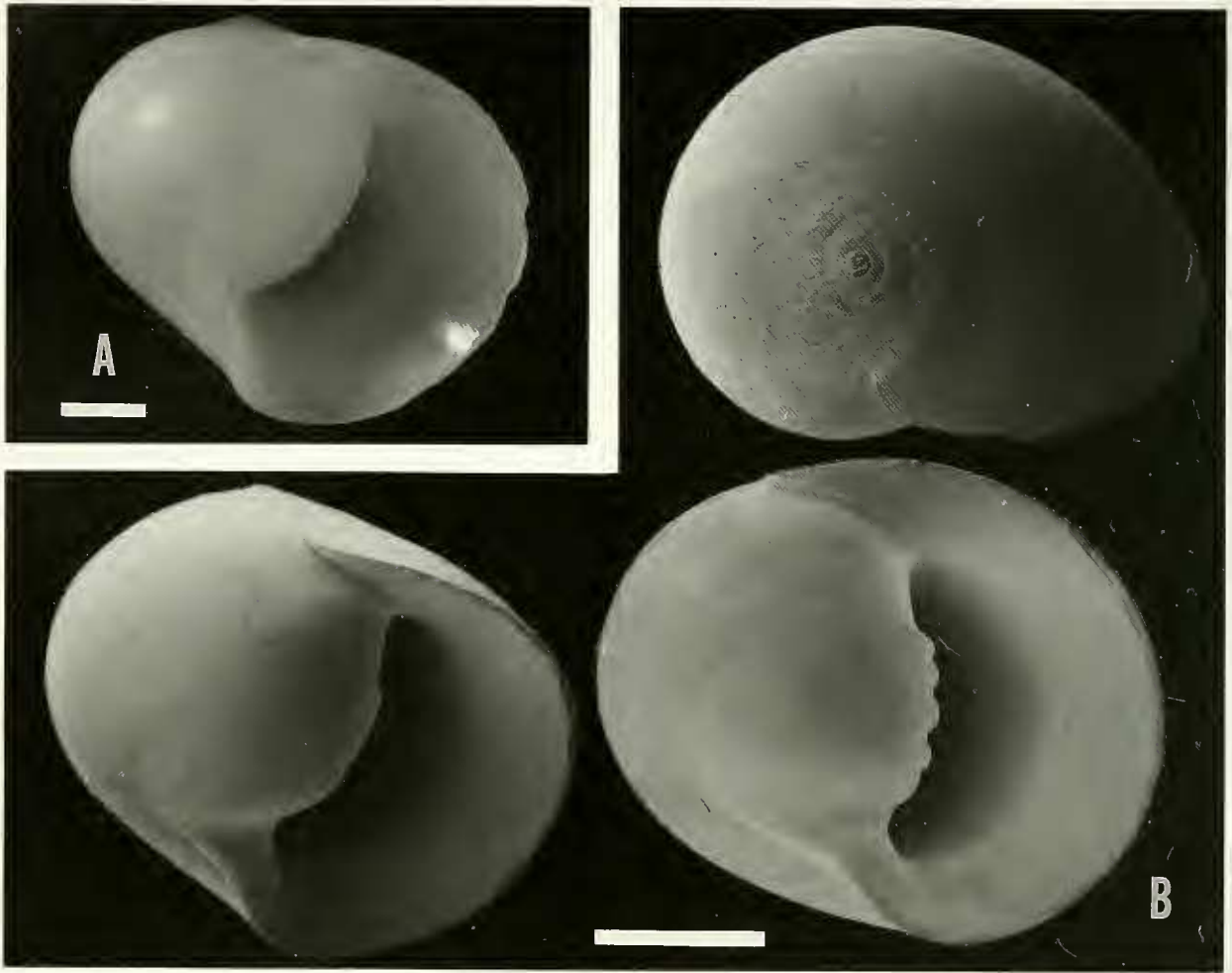


Figure 18. *Pisulina maxima* sp. nov. **A.** Holotype (NSMT-Mo71624) from Saipan. **B.** Paratype (NSMT-Mo71625) from Balicasag Island, Philippine Islands. Scale bars = 2 mm.

empty shells of this species in sediments from crevices north of Kohama Island in Okinawa Prefecture. The operculum of *P. biplicata* is almost identical to that of *P. adamsiana*.

Variation in shell characters is primarily manifested by the number and shape of teeth along the inner lip (Figure 17A). Specimens from Japan and the Philippines generally bear three squarish teeth, while those from Micronesian and southern Pacific islands commonly have more than three round teeth.

Japanese authors have long overlooked *P. biplicata* and misidentified it as *P. adamsiana* (Komatsu, 1986; Hinoide and Habe, 1991; Fukuda, 1993; Sasaki, 1998). Thiele (1925) established *P. biplicata* based on a single specimen and distinguished it from *P. adamsiana* by its supposed lower spire and the presence of two teeth on its inner lip. Unfortunately, these characters cannot be used to separate the two species, because the holotype of *P. biplicata* clearly is an immature specimen. The degree of spire elevation is highly dependent on growth stage, and mature *P. biplicata*

possess the highest spire in this genus. Also, the presence of only two teeth along the inner lip (Figures 16A; 17A-i) is attributed to the immature state of the holotype.

Examination of thousands of specimens from a number of localities clearly reveals that this species can easily be distinguished from *P. adamsiana* by the presence of a paucispiral protoconch, multiple teeth along the inner lip and a sinus in the inner line of the inner lip callus (Table 1). In addition, the shell surface of *P. biplicata* is covered with rows of microscopic granules, while that of *P. adamsiana* is covered with dense microscopic ridges (Figure 2A, B).

***Pisulina maxima* sp. nov.**

Figures 2C; 5C; 9; 17B; 18

Holotype.—NSMT-Mo71624, A huge cave near the "Grotto" diving site, on the northern side of Saipan Island, northern Mariana Islands (15°15.3'N, 145°49.5'N); 20–23.6 m depth.

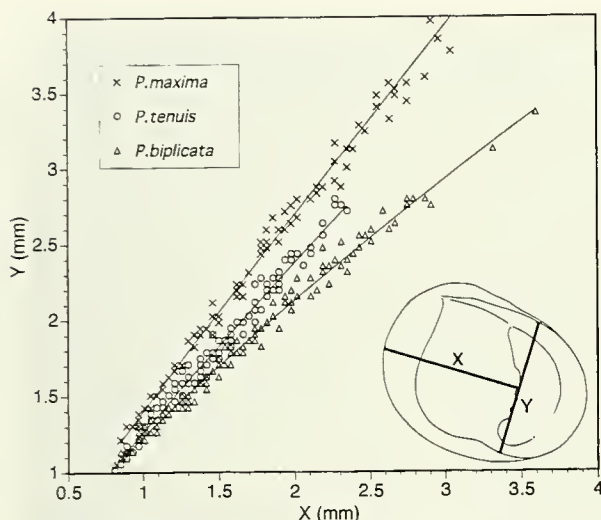


Figure 19. Relationship between the shape of the last whorl and the aperture in three *Pisulina* species: *Pisulina maxima* sp. nov. ($Y=1.668X^{0.945}$, $R^2=0.995$, $n=100$), *Pisulina tenuis* sp. nov. ($Y=1.650X^{0.914}$, $R^2=0.985$, $n=100$) and *Pisulina biplicata* Thiele ($Y=2.417X^{0.789}$, $R^2=0.989$, $n=100$). Specimens were measured in the following way under a microscope with a drawing attachment: X = apertural length from the abapertural margin of whorl to apertural teeth along the axis of the maximum dimension; Y = apertural height along an axis that is perpendicular to X and in contact with the apertural teeth. Shells used for measurements were selected arbitrarily to include all the ontogenetic stages greater than $Y = 1$ mm. Probabilities that the observed differences in the slopes of the growth lines arose by chance were calculated using a formula shown in Imbrie (1956). This figure shows that *P. biplicata* and *P. tenuis* are significantly different in having distinct slopes ($P < 0.01$); *P. maxima* and *P. tenuis* are meaningfully different ($0.01 < P < 0.05$). Nineteen specimens of *P. maxima* greater than 4 mm in the Y dimension are not plotted in this graph (the largest such specimen attains $Y = 7.53$ mm).

Paratypes.—JAPAN: Serakaki, Onna, Okinawa Island; 25 m depth, submarine cave; August 1998, 3 specimens, coll. H. Kinjo. —MALAYSIA: "Turtle Cavern", Sipadan Island, west Celebes Sea, Sabah ($5^{\circ}04.8'N$, $118^{\circ}36.5'E$); 9–17 m depth, totally dark inside; May 1997, 17 live individuals. —PHILIPPINES: "Marigondon Cave" diving site, Mactan Island, Cebu ($10^{\circ}15.8'N$, $123^{\circ}59.2'E$); 27 m depth, large submarine cave, totally dark inside; May 1994, 1 specimen. —Balicasag Island, Panglao, Bohol ($9^{\circ}32.7'N$, $123^{\circ}40.7'E$); 14–40 m depth, submarine caverns, gloomy inside; May 1994, 2 specimens (NSMT-Mo71625). —PALAU: "Siaes Tunnel" diving site, southwest of Siaes dropoff, ca. 6 km west-northwest of Aulong Island, Rock Islands ($7^{\circ}18.7'N$, $134^{\circ}13.6'E$); 24–53.5 m depth, huge submarine tunnel; April 1995, 65 specimens; December 1997, 148 specimens (30 specimens NSMT-Mo71626). —"Blue Hole" diving site, northwest of Ngemelis Island, Rock Islands ($7^{\circ}08.3'N$, $134^{\circ}13.3'E$); 36–38 m depth, submarine cave, totally dark inside; December 1997, 2 live individuals. —NORTHERN

MARIANAS: (the type locality); 12–30 m depth, huge cave, gloomy to totally dark inside; November 1997, 24 specimens (10 specimens NSMT-Mo71627); October 1999, 11 specimens. —near "Tinian Grotto" diving site, west of Tinian Island; 50–51 m depth, huge cave, gloomy to totally dark; November 1997, 3 specimens. —AUSTRALIA: "Thundercliff Cave" diving site, Christmas Island ($10^{\circ}28.4'S$, $105^{\circ}36.4'E$); 1.3–6 m depth, totally dark inside; November 1999, 4 specimens.

Distribution and age.—Southeast Asia (Figure 14). Recent.

Diagnosis.—Large *Pisulina* characterized by a subglobose to hemispherical and very thick shell, a paucispiral protoconch with an almost smooth surface, a large semicircular aperture and 3 to 7 teeth along inner lip; microscopic spiral ridges on shell surface are ca. 4 μ m wide.

Description.—Shell medium in size, up to 13.7 mm wide and 12.1 mm high (10.9 mm wide and 9.8 mm high in holotype), very thick, somewhat swollen hemispherical in shape (Figure 18); spire very low and apex pointed. Protoconch paucispiral, a simple low dome-shape in apical view, glossy, smooth, without inclination to teleoconch; visible portion surrounded by teleoconch 180 to 275 μ m in maximum dimension, ornamented by 15 to 25 indistinct longitudinal folds, with faint growth lines on outer lip (Figure 5C); protoconch aperture clearly demarcated from teleoconch by a sharp line. Teleoconch whorls less than 4 in number (3.8 in holotype), striated by microscopic growth lines and spiral ridges ca. 4 μ m wide (Figure 2C), the last whorl coiling nearly planispirally. Aperture semicircular, largely open, prosocline with an angle of 30° to 35° to shell axis; outer lip thick, widely beveled and slightly dilated outward; inner lip covered with a moderately thick callus, convex adaxially at middle, with 3 to 7 dull teeth (Figure 17B); inner line of inner lip callus convex at columellar area and continues to basal lip with shallow concavity. Operculum with a concentric nucleus ca. 220 μ m in maximum dimension (Figure 9C), and bears a long and spirally curved apophysis (Figure 9A, B).

Remarks.—This new species is similar in protoconch morphology to *P. biplicata*, but is primarily distinguished from the latter by its much larger shell size and less glossy teleoconch surface. In addition, the whorls of *P. maxima* expand more rapidly than in *P. biplicata*, so that the former species has a lower spire and a larger aperture than the latter species (Figure 19). This species further differs from *P. biplicata* in the number and shape of the inner lip teeth: *P. maxima* has up to seven rounded teeth, with the largest one located centrally, whereas *P. biplicata* has less than five squarish teeth, with the largest tooth located adapically. In addition, the third tooth ontogenetically appears above the first and second ones in the new species, while it appears below them in *P. biplicata* (Figure 17).

***Pisulina tenuis* sp. nov.**

Figures 2D; 5D, E; 17C; 20

Holotype.—NSMT-Mo71628, "Sabachi Cave," southeast of Yonaguni Island, Yaeyama Islands, Okinawa, Japan ($24^{\circ}26.1'N$, $122^{\circ}57.5'E$); 25–30 m depth, submarine cave,

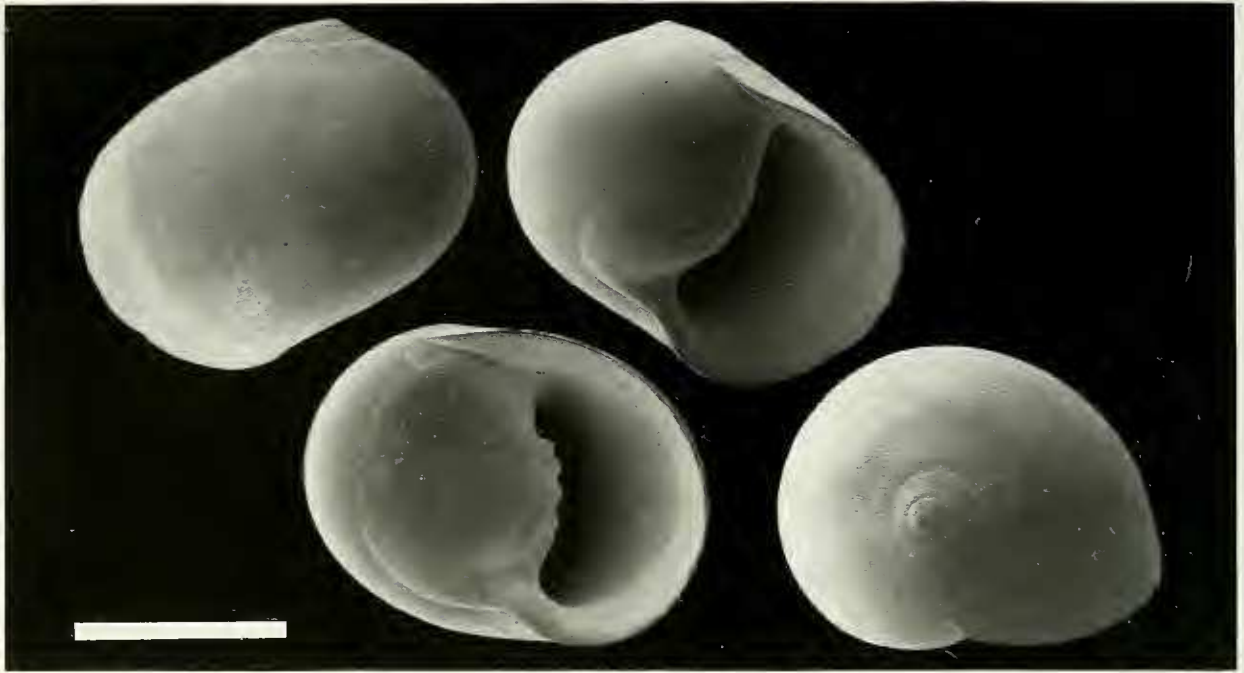


Figure 20. *Pisulina tenuis* sp. nov. Holotype (NSMT-Mo71628) from Yonaguni Island, Okinawa. Scale bar = 2 mm.

totally dark inside.

Paratypes.—More than 1000 specimens from the type locality; September 1994 (100 specimens registered; NSMT-Mo71629).

Distribution and age.—Known only from Yonaguni Island, Japan (Figure 14). Recent.

Diagnosis.—Small *Pisulina* characterized by a thin shell, subglobose to swollen hemispherical shape, a moderately large semicircular aperture, and 4 or 5 teeth along inner lip. Protoconch paucispiral, ovate and smooth. Teleoconch surface with spiral ridges ca. 4 μ m wide.

Description.—Shell small, 4.0 mm wide and 3.6 mm high in largest specimen (3.9 mm wide and 3.5 mm high in holotype), obliquely ovate to hemispherical in shape, and thin but solid. Spire low, with a pointed apex (Figure 20). Protoconch paucispiral, smooth except for 15 to 25 indistinct longitudinal folds near suture, glossy, ca. 330 μ m wide and ca. 270 μ m high, coils almost planispirally, and not inclined to teleoconch (Figure 5D, E); visible portion surrounded by teleoconch 210 to 300 μ m in maximum dimension (ca. 210 μ m in holotype); outer lip sculptured with indistinct growth lines and ridges (Figure 5D); protoconch aperture demarcated clearly from teleoconch and weakly sinuous in its middle part. Teleoconch coils up to 2.9 in number (2.8 in holotype), slightly concave below suture; exterior surface smooth except for faint growth lines and microscopic spiral ridges ca. 4 μ m wide (Figure 2D). Aperture semicircular in shape and widely open; outer lip prosocline, angled 35° to 40° from shell axis, weakly beveled and somewhat thickened on interior; inner lip moderately thick, bearing a convex

adaxial margin and 4 or 5 dull teeth of almost equal strength (Figure 17C); inner line of inner lip callus convex in columellar area and continues to basal lip with a shallow sinus.

Remarks.—*Pisulina tenuis* sp. nov. most closely resembles *P. maxima*, since both species share the same protoconch morphology, shell form and surface microsculpture. The two species are also similar in the number and shape of the inner lip teeth. However, *P. tenuis* clearly differs from *P. maxima* by its thinner shell and smaller shell size (see Table 1). A morphometric analysis shows that *P. tenuis* differs from *P. maxima* in having a smaller Y/X ratio (Figure 19).

Pisulina tenuis has not yet been found alive. Opercula thought to belong to this species were found among a vast number of empty shells at the type locality. The opercular features of *P. tenuis* are the same as seen in *P. adamsiana* and *P. maxima*.

Pisulina sp.

Figure 21

Material examined.—North Beach, Henderson Island, Pitcairn Group; middle or late Pleistocene sediments in an uplifted cave; 2 specimens, coll. R. C. Preece (Pitcairn Islands Scientific Expedition 1991–2), UMZC.

Distribution and age.—Known only from Henderson Island. Middle or late Pleistocene.

Description.—Shell small, thick, up to 4.2 mm wide and 3.8 mm high, hemispherical in outline (Figure 21A). Spire

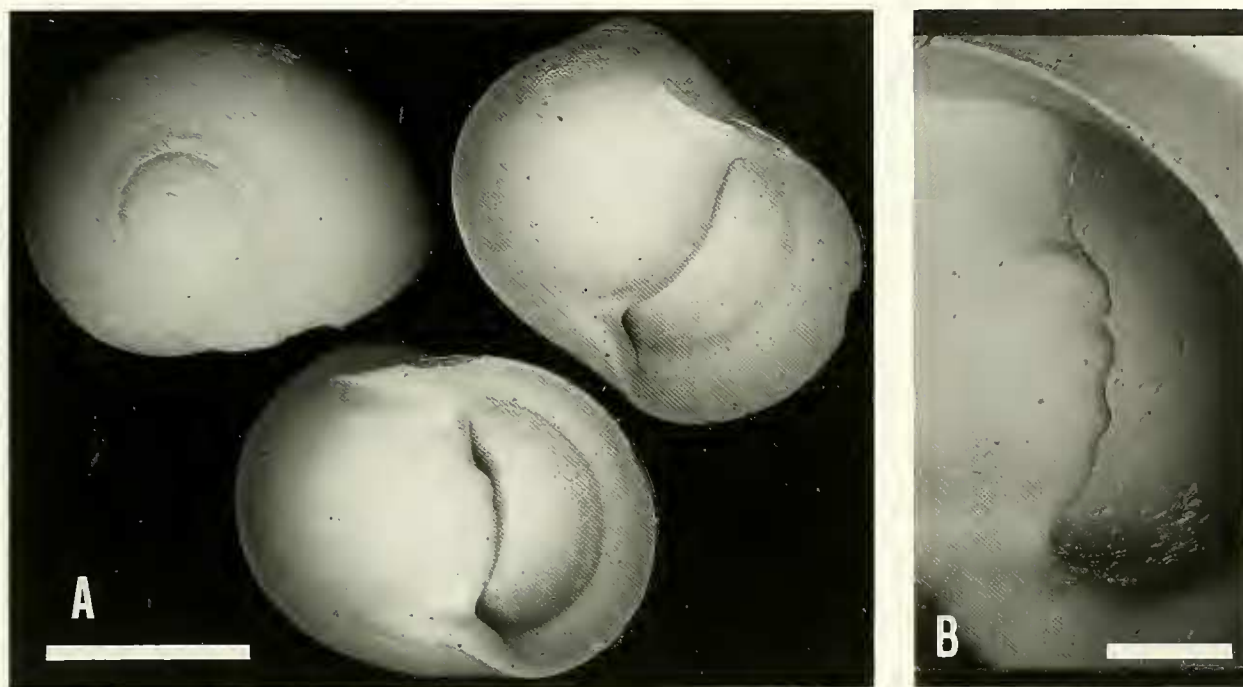


Figure 21. *Pisulina* sp. from Henderson Island, Pitcairn Group (UMZC). **A.** Scale bar = 2 mm. **B.** Oblique apertural view showing details of apertural teeth. Scale bar = 500 μ m.

relatively high, with a protruding apex. Protoconch poorly preserved, smooth, a simple dome-shape, 205 to 240 μ m in maximum dimension and sunken into teleoconch. Teleoconch of up to 3.1 volutions, concave below suture; exterior surface eroded to some extent, but seemingly smooth except for indistinct growth lines. Aperture semicircular and large; outer lip prosocline, angled about 35° to shell axis, beveled and slightly expanded outward; inner lip covered with a moderately thick callus, roundly convex with 4 dull teeth at margin (Figure 21B); inner line of inner lip callus merges into basal lip with a shallow sinus.

Remarks.—This unnamed Pleistocene species is similar to *P. tenuis* in shell size, the shape of its teleoconch whorls, and the number and shape of the teeth on the inner lip (Figure 21B). Moreover, both species have almost the same dimensions for the portion of the protoconch exposed above the teleoconch whorls. This fossil species seems to be distinct from *P. tenuis* by its thicker shell and higher spire, but it is left unnamed until better preserved material is available.

Several fossil specimens similar to this unnamed fossil species have been collected from early to middle Pleistocene sediments on Niue, Cook Islands, by G. Paulay. They differ slightly from *Pisulina* sp. by having a lower spire and fewer teeth on the inner lip, and by the absence of a concavity below the suture of the teleoconch whorls. However, the specimens from Niue cannot be compared in detail, owing to their poor state of preservation.

Acknowledgments

The materials in this paper were collected during the submarine cave expeditions in the tropical Pacific islands for the last 10 years directed by the second author. Special thanks are due to S. Ohashi and S. Kinjo who joined all the expeditions as members and dove many deep caves. Without doubt, our expeditions would have failed had it been without their self-sacrificing cooperation. Other members of the expedition include I. Hayami (Kanagawa University) and G. Paulay (University of Guam), to whom we are acknowledged. We thank the following persons who helped us in various ways: M. Cathrein (Christmas), K. Ekawa (Kagoshima), A. Fielding (Hawai'i), R. Gibson (Vanuatu), S. Gori (Italy), B. Holthuis (Guam), H. Kinjo (Okinawa), H. Kubo (Okinawa), C. Meyer (Guam), K. Mochizuki (Palau), K. Ogura (Okinawa), H. Saito (NSMT), M. Severns (Hawai'i), J. Starmer (Palau), M. Taniguchi (Okinawa) and Y. Yamazaki (Palau). ORSTOM (Noumea) and the University of the South Pacific gave facilities and logistic support for our expeditions in New Caledonia and Fiji, respectively. We also thank the following for the loan of materials: M. Glaubrecht (MNHB), I. Loch (AMS) and J. Thompson (USNM). This study was supported by grants to T. K. from the Ministry of Education, Science and Culture, Japan (nos. 06454003, 08041162, 11691196 and 11833018), the Fujiwara Natural History Foundation, and the Research Institute of Marine Invertebrates.

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